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THE HUMAN BODY

AN ACCOUNT OF

ITS STRUCTURE AND ACTIVITIES AND THE CONDITIONS OF ITS HEALTHY WORKING

BY

H. NEWELL MARTIN, D.Sc., M.A., M.D., F.R.S.

*Late Professor of Biology in the Johns Hopkins University
and of Physiology in the Medical Faculty
of the same*

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PUBLISHERS' NOTE.

THE Appendix on Reproduction of the earlier editions appears in this as Chapter XXXIX. Copies of the book without the chapter can be had when specially ordered.

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PREFACE TO THE SEVENTH EDITION.

THIS edition has been very thoroughly worked over and, I trust, improved. A considerable amount of new matter has been added, especially in connection with the cardiac and vascular nerves, and the physiology of the brain; but throughout the whole book many paragraphs have been re-written; and many corrections, rendered necessary by the discoveries of the last three or four years, have been made. I hope therefore that the edition will be found as well up to date as it is possible for a text-book to be: for a text-book must always incline to the conservative side, and deal with well-established facts rather than with even the most fascinating novelties. Still, as in previous editions, I have tried to show where the outposts and the outlooks of Physiology are.

H. N. M.

May 1, 1896.

PREFACE TO THE FIRST EDITION.

In the following pages I have endeavored to give an account of the structure and activities of the Human Body, which, while intelligible to the general reader, shall be accurate, and sufficiently minute in details to meet the requirements of students who are not making Human Anatomy and Physiology subjects of special advanced study. Wherever it seemed to me really profitable, hygienic topics have also been discussed, though at first glance they may seem less fully treated of than in many School or College Text-books of Physiology. Whoever will take the trouble, however, to examine critically what passes for Hygiene in the majority of such cases will, I think, find that, when correct, much of it is platitude or truism: since there is so much that is of importance and interest to be said it seems hardly worth while to occupy space with insisting on the commonplace or obvious.

It is hard to write a book, not designed for specialists, without running the risk of being accused of dogmatism, and some readers will, no doubt, be inclined to think that, in several instances, I have treated as established facts matters which are still open to discussion. General readers and students are, however, only bewildered by the production of an array of observations and arguments on each side of every question, and, in the majority of cases, the chief responsibility under which the author of a text-book lies is to select what seem to him the best supported views, and then to state them simply and concisely: how wise the choice of a side has been in each case can only be determined by the discoveries of the future.

Others will, I am inclined to think, raise the contrary objection that too many disputed matters have been dis-

cussed: this was deliberately done as the result of an experi-
ence in teaching Physiology which now extends over more
than ten years. It would have been comparatively easy to
slip over things still uncertain and subjects as yet unin-
vestigated, and to represent our knowledge of the workings
of the animal body as neatly rounded off at all its contours
and complete in all its details—*totus, teres, et rotundus.*
But by so doing no adequate idea of the present state of
physiological science would have been conveyed; in many
directions it is much farther travelled and more completely
known than in others; and, as ever, exactly the most inter-
esting points are those which lie on the boundary between
what we know and what we hope to know. In gross Anatomy
there are now but few points calling for a suspension of judg-
ment; with respect to Microscopic Anatomy there are more;
but a treatise on Physiology which would pass by, unmen-
tioned, all things not known but sought, would convey an
utterly unfaithful and untrue idea. Physiology has not fin-
ished its course. It is not cut and dried, and ready to be
laid aside for reference like a specimen in an Herbarium, but
is comparable rather to a living, growing plant, with some
stout and useful branches well raised into the light, others
but part grown, and many still represented by unfolded buds.
To the teacher, moreover, no pupil is more discouraging than
the one who thinks there is nothing to learn; and the boy
who has " finished " Latin and " done " Geometry finds some-
times his counterpart in the lad who has " gone through "
Physiology. For this unfortunate state of mind many Text-
books are, I believe, much to blame: difficulties are too often
ignored, or opening vistas of knowledge resolutely kept out of
view: the forbidden regions may be, it is true, too rough for
the young student to be guided through, or as yet pathless
for the pioneers of thought; but the opportunity to arouse
the receptive mental attitude apt to be produced by the rec-
ognition of the fact that much more still remains to be learned
—to excite the exercise of the reasoning faculties upon dis-
puted matters—and, in some of the better minds, to arouse
the longing to assist in adding to knowledge, is an inesti-
mable advantage, not to be lightly thrown aside through the
desire to make an elegantly symmetrical book. While I
trust, therefore, that this volume contains all the more impor-
tant facts at present known about the working of our Bodies,

I as earnestly hope that it makes plain that very much is yet to be discovered.

A work of the scope of the present volume is, of course, not the proper medium for the publication of novel facts; but, while the " Human Body," accordingly, professes to be merely a compilation, the introduction of constant references to authorities would have been out of place. I trust, however, that it will be found throughout imbued with the influence of my beloved master, Michael Foster; and on various hygienic topics I have to acknowledge a special indebtedness to the excellent series entitled *Health Primers.*

The majority of the anatomical illustrations are from Henle's *Anatomie des Menschen,* and a few from Arendt's *Schulatlas,* the publishers of each furnishing electrotypes. A considerable number, mainly histological, are from *Quain's Anatomy,* and a few figures are after Bernstein, Carpenter, Frey, Haeckel, Helmholtz, Huxley, McKendrick, and Wundt. About thirty, chiefly diagrammatic, were drawn specially for the work.

Quantities are throughout expressed first on the metric system, their approximate equivalents in American weights and measures being added in brackets.

H. NEWELL MARTIN.

BALTIMORE, October, 1880.

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CHAPTER XXXIX.

REPRODUCTION.

THE HUMAN BODY.

CHAPTER I.

THE GENERAL STRUCTURE AND COMPOSITION OF THE HUMAN BODY.

Definitions. The living Human Body may be considered from either of two aspects. Its structure may be especially examined, and the forms, connections and mode of growth of its parts be studied, as also the resemblances or differences in such respects which appear when it is compared with other animal bodies. Or the living Body may be more especially studied as an organism presenting definite properties and performing certain actions; and then its parts will be investigated with a view to discovering what duty, if any, each fulfils. The former group of studies constitutes the science of Anatomy, and in so far as it deals with the Human Body alone, of *Human Anatomy;* while the latter, the science concerned with the uses—or in technical language the *functions* —of each part is known as *Physiology.* Closely connected with physiology is the science of *Hygiene,* which is concerned with the conditions which are favorable to the healthy action of the various parts of the Body; while the activities and structure of the diseased body form the subject-matters of the sciences of *Pathology* and *Pathological Anatomy.*

Tissues and Organs. Histology. Examined merely from the outside our Bodies present a considerable complexity of structure. We easily recognize distinct parts as head, neck, trunk and limbs; and in these again smaller constituent parts, as eyes, nose, ears, mouth; arm, forearm, hand; thigh, leg and foot. We can, with such an external examination, go even farther and recognize different materials as entering into the formation of the larger parts. Skin, hair, nails and teeth are obviously different substances; simple examination

by pressure proves that internally there are harder and softer solid parts; while the blood that flows from a cut finger shows that liquid constituents also exist in the Body. The conception of complexity which may be thus arrived at from external observation of the living, is greatly extended by dissection of the dead Body, which makes manifest that it consists of a great number of diverse parts or *organs*, which in turn are built up of a limited number of materials; the same material often entering into the composition of many different organs. These primary building materials are known as the *tissues*, and that branch of anatomy which deals with the characters of the tissues and their arrangement in various organs is known as *Histology;* or, since it is mainly carried on with the aid of the microscope, as *Microscopic Anatomy.* If, with the poet, we compare the Body to a house, we may go on to liken the tissues to the bricks, stone, mortar, wood, iron, glass and so on, used in building; and then walls and floors, stairs and windows, formed by the combination of these, would answer to anatomical organs.

Zoological Position of Man. External examination of the human Body shows also that it presents certain resemblances to the bodies of many other animals: head and neck, trunk and limbs, and various minor parts entering into them, are not at all peculiar to it. Closer study and the investigation of internal structure demonstrates further that these resemblances are in many cases not superficial only, but that our Bodies may be regarded as built upon a plan common to them and the bodies of many other creatures: and it soon becomes further apparent that this resemblance is greater between the Human Body and the bodies of ordinary four-footed beasts, than between it and the bodies of birds, reptiles or fishes. Hence, from a zoological point of view, man's Body marks him out as belonging to the group of Mammalia (see Zoology), which includes all animals in which the female suckles the young ; and among mammals the anatomical resemblances are closer and the differences less between man and certain apes than between man and the other mammals; so that zoologists still, with Linnæus, include man with the monkeys and apes in one subdivision of the Mammalia, known as the *Primates.* That civilized man is mentally far superior to any other animal is no valid objection to such a classification, for zoological groups are defined by anatomical and not by

physiological characters; and mental traits, since we know that their manifestation depends upon the structural integrity of certain organs, are especially phenomena of function and therefore not available for purposes of zoological arrangement.

As man walks erect with the head upward, while the great majority of Mammals go on all fours with the head forward and the back upward, and various apes adopt intermediate positions, confusion is apt to arise in considering corresponding parts in man and other animals unless a precise meaning be given to such terms as "anterior" and "posterior." Anatomists therefore give those words definite arbitrary significations. The head end is always *anterior* whatever the natural position of the animal, and the opposite end *posterior;* the belly side is spoken of as *ventral,* and the opposite side as *dorsal; right* and *left* of course present no difficulty: the terms *cephalic* and *caudal* as equivalent, respectively, to anterior and posterior, are sometimes used. Moreover, that end of a limb nearer the trunk is spoken of as *proximal* with reference to the other or *distal* end. The words *upper* and *lower* may be conveniently used for the relative position of parts in the natural standing position of the animal.

The Vertebrate Plan of Structure. Neglecting such merely apparent differences as arise from the differences of normal posture above pointed out, we find that man's own zoological class, the Mammals, differs very widely in its broad structural plan from the groups including sea-anemones, insects or oysters, but agrees in many points with the groups of fishes, amphibians, reptiles and birds. These four are therefore placed with man and all other Mammals in one great division of the animal kingdom known as the *Vertebrata.* The main anatomical character of all vertebrate animals is the presence in the trunk of the body of two cavities, a dorsal and a ventral, separated by a solid partition; in the adults of nearly all vertebrate animals a hard axis, the *vertebral column* (*backbone* or *spine*), develops in this partition and forms a central support for the rest of the body (Fig. 2, *ee*). The dorsal cavity is continued through the neck, when there is one, into the head, and there widens out. The bony axis is also continued through the neck and extends into the head in a modified form. The ventral cavity, on the other hand, is confined to the trunk. It contains the main organs con-

nected with the blood-flow and is often called the *hæmal cavity.*

Upon the ventral side of the head is the *mouth-opening* leading into a tube, the *alimentary canal, f,* which passes back through the neck and trunk and opens again on the outside at the posterior part of the latter. In its passage through the trunk-region this canal lies in the ventral cavity.

The Mammalia. In many vertebrate animals the ventral cavity is not subdivided, but in the Mammalia it is; a

Fig. 1.—The Body opened from the front to show the contents of its ventral cavity. *lu,* lungs; *h,* heart, partly covered by other things; *la, la',* right and left liver-lobes respectively ; *ma,* stomach ; *ne,* the great omentum, a membrane containing fat which hangs down from the posterior border of the stomach and covers the intestines.

membranous transverse partition, the *midriff* or *diaphragm* (Fig. 1, *z*), separating it into an anterior *chest* or *thoracic*

cavity, and a posterior or *abdominal cavity.* The alimentary canal and whatever else passes from one of these cavities to the other must therefore perforate the diaphragm.

In the chest, besides part of the alimentary canal, lie important organs, the *heart, h,* and *lungs, lu;* the heart being on the ventral side of the alimentary canal. The abdominal cavity is mainly occupied by the alimentary canal and organs connected with it and concerned in the digestion of food, as the *stomach, ma,* the *liver, ls,* the *pancreas,* and the *intestines.* Among the other more prominent organs in it are the *kidneys* and the *spleen.*

In the dorsal or neural cavity lie the *brain* and *spinal cord,* the former occupying its anterior enlargement in the head. Brain and spinal cord together form the *cerebro-spinal nervous centre;* in addition to this there are found in the ventral cavity a number of small nerve-centres united together by connecting cords, and with their offshoots forming the *sympathetic nervous system.*

The walls of the three main cavities are lined by smooth, moist *serous membranes.* That lining the dorsal cavity is the *arachnoid;* that lining the chest the *pleura;* that lining the abdomen the *peritoneum;* the abdominal cavity is in consequence often called the peritoneal cavity. Externally the walls of these cavities are covered by the *skin,* which consists of two layers: an outer

.e

Fig. 2.—Diagrammatic longitudinal section of the body. *a,* the neural tube, with its upper enlargement in the skull-cavity at *a';* N, the spinal cord; N', the brain; *ee,* vertebræ forming the solid partition between the dorsal and ventral cavities; *b,* the pleural, and *c,* the abdominal division of the ventral cavity, separated from one another by the diaphragm, *d:* i, the nasal, and *o,* the mouth chamber, opening behind into the pharynx from which one tube leads to the lungs, *l,* and another to the stomach, *f:* h, the heart; *k,* a kidney; *s,* the sympathetic nervous chain. From the stomach, *f,* the intestinal tube leads through the abdominal cavity to the posterior opening of the alimentary canal.

horny layer called the *epidermis,* which is constantly being shed on the surface and renewed from below; and a deeper layer, called the *dermis* and containing blood, which the

epidermis does not.   Between the skin and the lining serous membranes are *bones, muscles* (the lean of meat), and a great number of other structures which we shall have to consider hereafter.   All cavities inside the body, as the alimentary canal and the air-passages, which open directly or indirectly on the surface are lined by soft and moist prolongations of the skin known as *mucous membranes.*   In these two layers are found as in the skin, but the superficial bloodless one is called *epithelium* and the deeper vascular one *corium.*

Diagrammatically we may represent the Human Body in longitudinal section as in Fig. 2, where *aa'* is the dorsal or *neural cavity,* and *b* and *c,* respectively, the thoracic and abdominal subdivisions of the ventral cavity; *d* represents the diaphragm separating them; *ee* is the vertebral column with its modified prolongation into the head beneath the anterior enlargement of the dorsal cavity; *f* is the alimentary canal opening in front through the nose, *i,* and mouth, *o*; *h* is the heart, *l* a lung, *s* the sympathetic nervous system, and *k* a kidney.

A transverse section through the chest is represented by the diagram Fig. 3, where *x* is the neural canal containing the spinal cord.   In the thoracic cavity are seen the heart, *h,*

Fɪɢ. 3.—A diagrammatic section across the Body in the chest region. *x,* the dorsal tube, which contains the spinal cord; the black mass surrounding it is a vertebra; *a,* the gullet, a part of the alimentary canal; *h,* the heart; *sy,* sympathetic nervous system; *ll,* lungs; the dotted lines around them are the pleuræ; *rr,* ribs; *st,* the breast-bone.

the lungs, *ll,* part of the alimentary canal, *a,* and the sympathetic nerve-centres, *sy ;* the dotted line on each side covering the inside of the chest-wall and the outside of the lung represents the *pleura.*

Sections through corresponding parts of any other Mammal would agree in all essential points with those represented in Figs. 2 and 3.

The Limbs.   The limbs present no such arrangement of cavities on each side of a bony axis as is seen in the trunk. They have an axis formed at different parts of one or more bones (as seen at *U* and *R* in Fig. 4, which represents a cross-section of the forearm near the elbow-joint), but around this are closely-packed soft parts, chiefly muscles, and the whole is enveloped in skin.   The only cavities in the limbs are branching tubes which are filled with liquids during life, either *blood* or a watery-looking fluid known as *lymph*.   These tubes, the *blood* and *lymph vessels* respectively, are not, how-

Fig. 4.—A section across the forearm a short distance below the elbow-joint. *R* and *U*, its two supporting bones, the radius and ulna; *e*, the epidermis, and *d*, the dermis of the skin; the latter is continuous below with bands of connective tissue, *s*, which penetrate between and invest the muscles, which are indicated by numbers; *n n*, nerves and vessels.

ever, characteristic of the limbs, for they are present in abundance in the dorsal and ventral cavities and in their walls.

Chemical Composition of the Body.   In addition to the study of the Body as composed of tissues and organs which are optically recognizable, we may consider it as composed of a number of different chemical substances.   This branch of knowledge, which is still very incomplete, really presents two classes of problems.   On the one hand we may limit ourselves to the examination of the chemical substances which exist in or may be derived from the dead Body, or, if such a thing were possible, from the living Body entirely at rest; such a study is essentially one of structure and may be called *Chemical Anatomy.*   But as long as the Body is alive it is the seat of constant chemical transformations in its material, and these are inseparably connected with its functions, the great majority of which are in the long-run dependent upon chemical changes.   From this point of view, then, the chemical study of the Body presents physiological problems, and it is usual to include all the facts known as to the chemical composition and metamorphoses of living matter under the name

of *Physiological Chemistry.* For the present we may confine ourselves to the more important substances derived from or known to exist in the Body, leaving questions concerning the chemical changes taking place within it for consideration along with those functions which are performed in connection with them.

Elements Composing the Body. Of the elements known to chemists only sixteen have been found to take part in the formation of the human Body. These are carbon, hydrogen, nitrogen, oxygen, sulphur, phosphorus, chlorine, fluorine, silicon, sodium, potassium, lithium, calcium, magnesium, iron and manganese. Copper and lead have sometimes been found in small quantities, but are probably accidental and occasional.

Uncombined Elements. Only a very small number of the above elements exist in the Body uncombined. *Oxygen* is found in small quantity dissolved in the blood; but even there most of it is in a state of loose chemical combination. It is also found in the cavities of the lungs and alimentary canal, being derived from the inspired air or swallowed with food and saliva; but while contained in these spaces it can hardly be said to form a part of the Body. *Nitrogen* also exists uncombined in the lungs and alimentary canal, and in small quantity in solution in the blood. Free *hydrogen* has also been found in the alimentary canal, being there evolved by the fermentation of certain foods.

Chemical Compounds. The number of these which may be obtained from the Body is very great; but with regard to very many of them we do not know that the form in which we extract them is really that in which the elements they contain were united while in the living Body; since the methods of chemical analysis are such as always break down the more complex forms of living matter and leave us only its *débris* for examination. We know in fact, tolerably accurately, what compounds enter the Body as food and what finally leave it as waste; but the intermediate conditions of the elements contained in these compounds during their sojourn inside the Body we know very little about; more especially their state of combination during that part of their stay when they do not exist dissolved in the bodily liquids, but form part of a solid living tissue.

For present purposes the chemical compounds existing in

or derived from the Body may be classified as organic and inorganic, and the former be subdivided into those which contain nitrogen and those which do not.

Nitrogenous or Azotized Organic Compounds. These fall into several main groups: *proteids, peptones, albuminoids, enzymes, crystalline substances,* and *coloring matters.*

Proteids are by far the most characteristic substances obtained from the Body, since they are only known as existing in or derived from living things, either animals or plants. The type of this class of bodies may be found in the white of an egg, where it is stored up as food for the developing chick; from this typical form, which is called *egg-albumin,* the proteids in general are often called *albuminous bodies.* Each of them contains carbon, hydrogen, oxygen, sulphur and nitrogen united to form a very complex molecule, and although different members of the family differ from one another in minor points they all agree in their broad features and have a similar percentage composition. The latter in different examples varies within the following limits:

Carbon	50 to	55	per cent.
Hydrogen	6.8 to	7.3	"
Oxygen	22.8 to	24.1	"
Nitrogen	15.4 to	18.2	"
Sulphur	0.4 to	5.0	"

In addition a small quantity of ash is usually left when a proteid is burnt.

Proteids are recognized by the following characters:

1. Boiled, either in the solid state or in solution, with strong nitric acid they give a yellow liquid which becomes orange on neutralization with ammonia. This is the *xantho-proteic test.*

2. Boiled with a solution containing subnitrate and pernitrate of mercury they give a pink precipitate, or, if in very small quantity, a pink-colored solution. This is known as *Millon's test.*

3. If a solution containing a proteid be strongly acidulated with acetic acid and be boiled after the addition of an equal bulk of a saturated watery solution of sodium sulphate, the proteid will be precipitated.

Among the more important proteids obtained from the Human Body are the following:

Serum-albumin. This exists in solution in the blood and

is very like egg-albumin in its properties. It is coagulated (like the white of an egg) when boiled, and then passes into the state of *coagulated proteid* which is, unlike the original serum-albumin, insoluble in dilute acids or alkalies or in water containing neutral salts in solution. All other proteids can by appropriate treatment be turned into coagulated proteid.

Fibrin. This forms in blood when it "clots," either inside or outside of the Body; it is insoluble in water and dilute acids or alkalies; soluble in strong acids and alkalies and, though slowly, in ten per cent neutral saline solutions.

Myosin. This is derived from the muscles, in which it develops and solidifies after death, causing the "death-stiffening."

Globulin exists in the red globules of the blood and dissolved in some other liquids of the body. In the blood-corpuscles it is combined with a colored non-proteid substance to form *hæmoglobin,* which is crystallizable. Allied substances, *paraglobulin* and *fibrinogen,* are found dissolved in the blood-liquid. When blood clots the fibrinogen gives rise to *fibrin.*

Casein or, as it is better named, *caseinogen* exists in milk. Its solutions do not coagulate spontaneously or, like that of serum-albumin, on boiling. When milk turns sour on keeping, or when it is very slightly acidulated with dilute acetic acid, the casein is precipitated. The clot or curd which forms when milk is gently warmed with gastric juice or with rennet, is also derived from caseinogen; it differs from true casein and is named *tyrein:* it is the chief constituent of cheese.

Peptones. These are formed in the alimentary canal by the action of some of the digestive liquids upon the proteids swallowed as food. They contain the same elements as the proteids and give the xantho-proteic and Millon's reactions, but are not precipitated by boiling with acetic acid and sodium sulphate. Their great distinctive character is, however, their diffusibility. The proteids proper will not dialyze (see Physics), but the peptones in solution pass readily through moist animal membranes.

Albuminoids or Gelatinoids. These contain carbon, hydrogen, oxygen and nitrogen, but rarely any sulphur. Like the proteids, the nearest chemical allies of which they seem.

to be, they are only known in or derived from living beings. *Gelatin,* obtained from bones and ligaments by boiling, is a typical albuminoid; as is *chondrin,* which is obtained similarly from gristle. *Mucin,* which gives their glairy tenacious character to the secretions of the mouth and nose, is another albuminoid.

Enzymes or Soluble Ferments are a group of substances which seem to be allied in chemical composition to the true proteids, but it is so difficult to be sure of the purity of any specimen that their composition is still in doubt. The *enzymes* have the power, even when present in very small quantity, of bringing about extensive changes in other substances, and they are not themselves necessarily used up or destroyed in the process. Many enzymes of great physiological importance exist in the digestive fluids and play a part in fitting food for absorption from the alimentary canal. For example, *pepsin* found in the gastric juice and *trypsin* found in the pancreatic secretion convert, under suitable conditions, albuminous substances into peptones; and *ptyalin,* found in the saliva, converts starch into sugar. Other ferments cause the clotting of various animal liquids: *rennin* from the gastric juice clots the caseinogen of milk preparatory to its digestion; and a ferment which forms in drawn blood converts fibrinogen into fibrin. We shall have occasion later to study several enzymes more in detail in connection with their physiological uses.

Crystalline Nitrogenous Substances. These are a heterogeneous group, the great majority of them being materials which have done their work in the Body and are about to be got rid of. Nitrogen enters the Body in foods for the most part in the chemically complex form of some proteid. In the vital processes these proteids are broken down into simpler substances, their carbon being partly combined with oxygen and passed out through the lungs as carbon dioxide; their hydrogen is similarly in large part combined with oxygen and passed out as water; while their nitrogen, with some carbon and hydrogen and oxygen, is usually passed out in the form of a crystalline compound, containing what chemists call an "ammonium residue." Of these the most important is *urea* (Carbamide, $2NH_4,CO$), which is eliminated through the kidneys. *Uric acid* is another nitrogenous waste product, and many others, such as *kreatin* and *leucin,* seem to be inter-

mediate stages between the proteids which enter the body and the urea and uric acid which leave it.

In the bile or gall, two crystallizable nitrogen-containing bodies, *glycocholic* and *taurocholic acid,* are found combined with soda.

Nitrogenous Coloring Matters. These form an artificial group whose constitution and origin are ill known. Among the most important are the following:

Hæmatin, derived from the red corpuscles of the blood in which a residue of it is combined with a proteid residue to form *hæmoglobin.*

Bilirubin and *biliverdin,* which exist in the bile; the former predominating in the bile of man and of carnivorous animals and giving it a reddish-yellow color, while biliverdin predominates in the bile of Herbivora, which is green.

Non-Nitrogenous Organic Compounds. These may be conveniently grouped as *hydrocarbons* or fatty bodies; *carbohydrates* or *amyloids;* and certain *non-azotized acids.*

Fats. The *fats* all contain carbon, hydrogen and oxygen, the oxygen being present in small proportion as compared with the hydrogen. Three fats occur in the Body in large quantities, viz.: *palmatin* ($C_{81}H_{98}O_6$), *stearin* ($C_{87}H_{110}O_6$), and *olein* ($C_{87}H_{104}O_6$). The two former when pure are solid at the temperature of the Body, but in it are mixed with olein (which is liquid) in such proportions as to be kept fluid. The total quantity of fat in the Body is subject to great variations, but its average quantity in a man weighing 75 kilograms (165 pounds) is about 2.75 kilograms (6 pounds).

Each of these fats when heated with a caustic alkali, in the presence of water, breaks up into a fatty acid (*stearic, palmitic* or *oleic* as the case may be), and *glycerin.* The fatty acid unites with the alkali present to form a *soap.*

Carbohydrates. These also contain carbon, hydrogen and oxygen, but there is one atom of oxygen present for every two of hydrogen in the molecule of each of them. Chemically they are related to starch. The more important of them found in the Body are the following:

Glycogen ($C_6H_{10}O_5$), found in large quantities in the liver, where it seems to be a reserve of material answering to the starch stored up by many plants. It exists in smaller quantities in the muscles.

Glucose, or *grape-sugar* ($C_6H_{12}O_6$), which exists in **the**

liver in small quantities; also in the blood and lymph. It is largely derived from glycogen, which is very readily converted into it.

Lactose, or *sugar of milk* ($C_{12}H_{22}O_{11} + H_2O$), found in considerable quantity in milk.

Inosit ($C_6H_{12}O_6 + 2H_2O$), also called *muscle-sugar* and formerly classed in this group, is now known to be chemically not a real sugar or true carbohydrate. It exists in muscles, liver, spleen, kidneys, etc.

Organic Non-Nitrogenous Acids. Of these the most important is *carbon dioxide* (CO_2), which is the form in which by far the greater part of the carbon taken into the Body ultimately leaves it. United with calcium it is found in the bones and teeth in large proportion.

Formic, acetic and *butyric acids* are also found in the Body; stearic, palmitic, and oleic have been above mentioned as obtainable from fats. *Lactic acid* is sometimes found in the stomach, and when milk turns sour is formed from lactose. A body of the same percentage composition, $C_3H_6O_3$ (*sarco-lactic acid*), is formed in muscles when they work or die.

Glycerin phosphoric acid ($C_3H_9PO_6$) is obtained on the decomposition of *lecithin*, a complex nitrogenous fat found in nervous tissue.

Inorganic Constituents. Of the simpler substances entering into the structure of the Body the following are the most important :

Water ; in all the tissues in greater or less proportion and forming about two thirds of the weight of the whole Body. A man weighing 75 kilos (165 lbs.), if completely dried would therefore lose about 50 kilos (110 lbs.) from the evaporation of water. Of the constituents of the Body the enamel of the teeth contains least water (about 2 per cent), and the saliva most (about 99.5 per cent); between these extremes are all intermediate steps—bones containing about 22 per cent, muscles 75, blood 79.

Common salt—Sodium chloride—(NaCl); found in all the tissues and liquids, and in many cases playing an important part in keeping other substances in solution in water.

Potassium chloride (KCl); in the blood, muscles, nerves and most liquids.

Calcium phosphate ($Ca_3 2PO_4$); in the bones and teeth in large quantity. In less proportion in all the other tissues.

Besides the above, ammonium chloride, sodium and potassium phosphates, magnesium phosphate, sodium sulphate, potassium sulphate and calcium fluoride have been obtained from the body.

Uncombined *hydrochloric acid* (HCl) is found in the gastric juice.

CHAPTER II.

THE FUNDAMENTAL PHYSIOLOGICAL ACTIONS.

The Properties of the Living Body. When we turn from the structure and composition of the living Body to consider its powers and properties we meet again with great variety and complexity, the most superficial examination being sufficient to show that its parts are endowed with very different faculties. Light falling on the eye arouses in us a sensation of sight, but falling on the skin has no such effect; pinching the skin causes pain, but pinching a hair or a nail does not; when the ears are stopped, sounds arouse in us no sensation; we readily recognize, too, hard parts formed for support. joints to admit of movements, apertures to receive food and others to get rid of waste. We thus perceive that different organs of our Bodies have very different endowments and serve for very distinct purposes; and here also the study of internal organs shows us that the varieties of quality observed on the exterior are but slight indications of differences of property which pervade the whole, being sometimes dependent on the specific characters of the tissues concerned and sometimes upon the manner in which these are combined to form various organs. Some tissues are solid, rigid and of constant shape, as those composing the bones and teeth; others, as the muscles, are soft and capable of changing their forms; and still others are capable of working chemical changes by which such peculiar fluids as the bile and the saliva are produced. We find elsewhere a number of tissues combined to form a tube adapted to receive food and carry it through the Body for digestion, and again similar tissues differently arranged to receive the air which we breathe-in, and expel it after abstracting part of its oxygen and adding to it certain other things; and in the heart and blood-vessels we find almost the same tissues arranged to propel and carry the blood over the whole Body. The working of

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the Body offers clearly even a more complex subject of study than its structure.

Physiological Properties. In common with inanimate objects the Body possesses many merely physical properties, as weight, rigidity, elasticity, color, and so on; but in addition to these we find in it while alive many others which it ceases to manifest at death. Of these perhaps the power of executing spontaneous movements and of maintaining a high bodily temperature are the most marked. As long as the Body is alive it is warm and, since the surrounding air is nearly always cooler, must be losing heat all day long to neighboring objects; nevertheless we are at the end of the day as warm as at the beginning, the temperature of the Body in health not varying much from 37° C. (98.4° F.), so that clearly our Bodies must be making heat somehow all the time. After death this production of heat ceases and the Body cools down to the temperature in its neighborhood; but so closely do we associate with it the idea of warmth that the sensation experienced on touching a corpse produces so powerful an impression as commonly to be described as icy cold. The other great characteristic of the living Body is its power of executing movements; so long as life lasts it is never at rest; even in the deepest slumber the regular breathing, the tap of the heart against the chest-wall, and the beat of the pulse tell us that we are watching sleep and not death. If to this we add the possession of consciousness by the living Body, whether aroused or not by forces immediately acting upon sense-organs, we might describe it as a heat-producing, moving, conscious organism.

The production of heat in the Body needs fuel of some kind as much as its production in a fire; and every time we move ourselves or external objects some of the Body is used up to supply the necessary working power, just as some coals are burnt in the furnace of an engine for every bit of work it does; in the same way every thought that arises in us is accompanied with the destruction of some part of the Body. Hence these primary actions of keeping warm, moving, and being conscious, necessitate many others for the supply of new materials to the tissues concerned and for the removal of their wastes; still others are necessary to regulate the production and loss of heat in accordance with changes in the exterior temperature, to bring the moving tissues into rela-

tion with the thinking, and so on. By such subsidiary arrangements the working of the whole Body becomes so complex that it would fill many pages merely to enumerate what is known of the duties of its various parts. However, all the proper physiological properties depend in ultimate analysis on a small number of faculties which are possessed by all living things, their great variety in the human Body depending upon special development and combination in different tissues and organs; and before attempting to study them in their most complex forms it is advantageous to examine them in their simplest and most generalized manifestations, as exhibited by some of the lowest living things or by the simplest constituents of our own Bodies.

Cells. Among the anatomical elements which the histologist meets with as entering into the composition of the human Body are minute granular masses of a soft consistence, about 0.012 millimeter ($\frac{1}{2000}$ of an inch) in diameter (Fig. 5, *b*). Imbedded in each lies a central portion, not so granular and therefore different in appearance from the rest. These anatomical units are known as *cells*, the granular substance being the *cell-body* and the imbedded clearer portion the *cell-nucleus*. Inside the nucleus may

Fig. 5.—Forms of cells from the Body.

often be distinguished a still smaller body—the *nucleolus*. Cells of this kind exist in abundance in the blood, where they are known as the *white blood-corpuscles*, and each exhibits of itself certain properties which are distinctive of all living things as compared with inanimate objects.

Cell Growth. In the first place, each such cell can take up materials from its outside and build them up into its own peculiar substance; and this does not occur by the deposit of new layers of material like its own on the surface of the cell (as a crystal might increase in an evaporating solution of the same salt), but in an entirely different way. The cell takes up chemical elements, either free or combined in a manner different from that in which they exist in its own living substance, and works chemical changes in them by which they are made into part and parcel of itself. Moreover, the new material thus formed is not deposited, at any rate necessarily or always, on the surface of the old, but is laid down in the

substance of the already existing cell among its constituent
molecules. The new-formed molecules therefore contribute
to the growth of the cell not by superficial *accretion*, but by
interstitial deposit or *intussusception*.

Cell Division. The increase of size, which may be brought
about in the above manner, is not indefinite, but is limited in
two ways. Alongside of the formation and deposit of new
material there occurs always in the living cell a breaking
down and elimination of the old; and when this process

Fig. 6.—Diagrams illustrating direct cell-division. *a*, cell, body; *b*, nucleus;
c, nucleolus.

equals the accumulation of new material, as it does in all the
cells of the Body when they attain a certain size, *growth*
of course ceases. In fact the work of the cell increases
as its *mass*, and therefore as the cube of its diameter;
while the receptive powers, dependent primarily upon the
superficial area, only increase as the square of the diameter.
The breaking down in the cell increases when its work
does, and so comes at last to equal the reception and con-
struction. The second limitation to indefinite growth is
connected with the power of the cell to give rise to new cells
by *division*.

Until recently it was believed that cell division was in all
cases a comparatively simple process (Fig. 6). It was thought
that the nucleus, without any important structural change,
enlarged somewhat, became elongated, and then divided by
simple constriction into two equal parts, forming two smaller
daughter nuclei; and that the rest of the cell then divided,
its halves arranging themselves around the new nuclei. The
nucleolus when present was supposed to divide before the
nucleus. Such a mode of cell multiplication is known as
direct division: it possibly occurs in some cases, but in the
great majority of cells division is preceded by marked changes
in the structure of the nucleus and by a rearrangement of its
material: such cell division is named indirect, and the attend-
ant nuclear changes are known as the phenomena of *karyoki-
nesis* or *mitosi"*

Indirect, Karyokinetic or Mitotic Cell Division. Before attempting to describe the phenomena of indirect cell divisions it is necessary to give some account of the structure of a typical primitive cell as made out in specimens carefully prepared and studied with the highest powers of the microscope. The main bulk of the cell, surrounding the nucleus, is the *cell-body*, and in some cases is enclosed in an envelope or *sac*, which, however, when present, plays but a secondary or passive part in cell division. The cell-body, known also as

Fig. 7.—Diagram of an animal cell. *a*, hyaloplasm; *b*, reticulum; *c*, nucleus. *a* and *b* together form the cell-body.

the *cell-protoplasm* (Fig. 7), consists of a network of extremely fine threads, the *reticulum* or *spongioplasm*, the meshes of which are occupied by a different substance, the *hyaloplasm:* the proportions of hyaloplasm and spongioplasm vary in different cells and often in different parts of the same cell; in fact a layer of hyaloplasm unmixed with spongioplasm frequently exists on the exterior of the cell, and the hyaloplasm appears to be the more immediately concerned in the activities of the living cell. In addition there is to be found, imbedded in the cell-body and near the nucleus or attached to it, an extremely minute particle, the *attraction-particle* or *centrosome*, near which a radial arrangement of the cell-substance may often be observed.

The nucleus (Fig. 8) of a resting cell, that is of a cell not in process of division, consists of an amorphous material (*nucleoplasm*) which is perhaps similar in composition to the hyaloplasm, and a filamentous material, different from spongioplasm, and named *chromoplasm* or *karyoplasm*. As proved by its behavior with staining fluids and other

Fig. 8.—Diagram of a resting nucleus *a*, nuclear membrane; *b*, nucleoplasm; *c*, nucleolus; *d*, chromoplasm; *e*, some of the surrounding protoplasm of the cell, the structure of which is not indicated.

reagents karyoplasm is quite different chemically from the spongioplasm of the cell-body. One or more granules (*nucleoli*) which may be found within most nuclei are probably

local accumulations of chromoplasm; a membrane (*nuclear membrane*) which surrounds the nucleus of cells not in process of division is also probably composed of chromoplasm.

The first observed step in cell division is binary division of the attraction-particle: its halves evolve a set of very fine *achromatin filaments* uniting them, so that each half is one of the poles of a spindle-shaped collection of fibres, the *nuclear spindle.* Meanwhile the nucleolus and nuclear membrane disappear, being probably taken up into the rest of the chromoplasm, which now, instead of its original reticular arrange-

Fig. 9 – Diagrams of a nucleus in an early stage of karyokinesis. *A* showing the polar, *B* the antipolar region: *a*, nuclear or achromatin spindle. *b*, part of general cell protoplasm around the nucleus; *c*, looped chromatic filament; *d*, nucleoplasm.

ment, takes the form of a single long *chromatic filament* coiled in the nucleoplasm. At one portion of the nucleus (*pole*) the loops of the chromatic filament leave a space free from them (Fig. 9, *A*), and in the neighborhood of this space the nuclear spindle is first seen within the nucleus. At the opposite side of the nucleus or *antipole* (Fig. 9, *B*) the loops of the chromatic filament leave no clear space, but cross irregularly. In the next stage the loops at the antipolar end break through, and in this way the filament is divided into a number of irregular elongated Vs, each with its closed angle near the pole and its open end near the antipole. The spindle meanwhile passes to the centre of the nucleus and takes a position in which its long axis coincides with that joining pole and antipole, and then the Vs of chromoplasm become shorter and their limbs thicker, and they also shift position so as to group themselves radially around the equator of the spindle (*A*, Fig. 10) with their angles directed centrally. Each V then divides along its whole length, and one half passes towards the

pole, the other towards the antipole. The whole nucleus elongates in the direction of the long axis of the spindle; the achromatin filaments disappear, and the nucleus dividing in

B

Fig. 10.—Diagrams representing more advanced stages of karyokinesis than those illustrated in Fig. 9. *a,* polar, and *e,* antipolar end of nuclear spindle; *b* and *c,* portions of the chromatic filament; *d,* nucleoplasm; *f,* cell protoplasm with indications of a radial arrangement in the neighborhood of the pole and antipole.

The nuclear spindle is seen to have lengthened and become placed in the centre of the nucleus, the pole and antipole of which its ends reach. In *A* the Vs which resulted from divisions of the chromatic filament at its antipolar loops are seen to have become much shorter and thicker and to have changed position, so that instead of lying lengthwise in the nucleus, with their points towards the pole, they lie equatorially, with their points towards the spindle and their open ends towards the periphery of the nucleus. For the sake of clearness only two are represented out of the set of them which surrounds the spindle; *b* is still uncleft; *c* has nearly completed its longitudinal division into two Vs, the angle of one of which is commencing to travel towards the pole and of the other towards the antipole. In *B* the splitting of the Vs and the progress of their halves towards the ends of the nucleus is more advanced.

the equatorial plane, two nuclei are formed, each with nucleoplasm and chromoplasm: the chromoplasm of each is derived, as follows from the preceding description, from both polar and antipolar regions of the parent nucleus. The chromoplasm in each daughter nucleus unites into a single convoluted chromatic filament like that represented for the parent nucleus in Fig. 9, and this filament breaks up and becomes arranged into reticulum, nucleolus and nuclear membrane as in the resting cell (Figs. 7 and 8). Around the new nuclei the cell-protoplasm rearranges itself and divides to form a new cell-body enveloping each; during its rearrangement its material frequently presents a radial structure, the radii converging towards the ends of the nuclear spindle. The poles of the nuclear spindle, which it will be remembered represent the halves of

the original centrosome, probably pass out of the new nuclei and become the attraction particles of the new cells.

The phenomena of karyokinesis show clearly that in spite of its small size the animal cell is a complicated structure, made up of very distinct parts possessing very distinct properties and no doubt very different functions.

Assimilation: Reproduction. The two powers, that of working up into their own substance materials derived from outside, known as *assimilation*, and that of, in one way or another, giving rise to new beings like themselves, known as *reproduction*, are possessed by all kinds of living beings, whether animals or plants. There is, however, this important difference between the two: the power of assimilation is necessary for the maintenance of each individual cell, plant or animal, since the already existing living material is constantly breaking down and being removed as long as life lasts, and the loss must be made good if any of them is to continue its existence. The power of reproduction, on the other hand, is necessary only for the continuance of the kind or race, and need be, and often is, possessed only by some of the individuals composing it. Working bees, for example, cannot reproduce their kind, that duty being left to the queen-bee and the drones of each hive.

The breaking down of already existing chemical compounds into simpler ones, sometimes called *dissimilation*, is as invariable in living beings as the building up of new complex molecules referred to above. It is associated with the assumption of uncombined oxygen from the exterior, which is then combined directly or indirectly with other elements in the cell, as, for example, carbon, giving rise to carbon dioxide, or hydrogen, producing water. In this way the molecule in which the carbon and hydrogen previously existed is broken down and at the same time energy is liberated, which in all cases seems to take in part the form of heat just as when coal is burnt in a fire, but may be used in part for other purposes, such as producing movements. The carbon dioxide is usually got rid of by the same mechanism as that which serves to take up the oxygen, and these two processes constitute the function of *respiration* which occurs in all living things. Assimilation and dissimilation, going on side by side and being to a certain extent correlative, are often spoken of together as the process of *nutrition :* the assimilative or chemically constructive processes are also named *anabolic*, and the dissimilative *katabolic*.

Contractility. Nutrition and (with the above-mentioned partial exception) reproduction characterize all living creatures; and both faculties are possessed by the simple nucleated cells already referred to as found in our blood. But these cells possess also certain other properties which, although not so absolutely diagnostic, are yet very characteristic of living things. Examined carefully with a microscope in a fresh-drawn drop of blood, they exhibit changes of form independent of any pressure which might distort them or otherwise mechanically alter their shape. These changes may sometimes show themselves as constrictions ultimately leading to the division of the cell ; but more commonly (Fig. 15*) they have no such result, the cell simply altering its form by drawing in its substance at one point and thrusting it out at another. The portion thus protruded may in turn be drawn in and a process be thrown out elsewhere ; or the rest of the cell may collect around it, and a fresh protrusion be then made on the same side ; and by repeating this manœuvre these cells may change their place and creep across the field of the microscope. Such changes of form from their close resemblance to those exhibited by the microscopic animal known as the *Amœba* (see Zoology) are called *amœboid*, and the faculty in the living cell upon which they depend is known in physiology as *contractility*. It must be borne in mind that physiological contractility in this sense is quite different from the so-called contractility of a stretched india-rubber band, which merely tends to reassume a form from which it has previously been forcibly removed.

Irritability. Another property exhibited by these blood-cells is known as *irritability*. An Amœba coming into contact with a solid particle calculated to serve it as food will throw around it processes of its substance, and gradually carry the foreign mass into its own body. The amount of energy expended by the animal under these circumstances is altogether disproportionate to the force of the external contact. It is not that the swallowed mass pushes-in mechanically the surface of the Amœba, or burrows into it, but the mere touch arouses in the animal an activity quite disproportionate to the exciting force, and comparable to that set free by a spark falling into gunpowder or by a slight tap on a piece of gun-cotton. It is this disproportion between the excitant (known

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in Physiology as a *stimulus*) and the result, which is the essential characteristic of *irritability* when the term is used in a physiological connection. The granular cells of the blood can take foreign matters into themselves in exactly the same manner as an Amœba does; and in this and in other ways, as by contracting into rigid spheres under the influence of electrical shocks, they show that they also are endowed with irritability.

Conductivity. Further, when an Amœba or one of these blood-cells comes into contact with a foreign body and proceeds to draw it into its own substance, the activity excited is not merely displayed by the parts actually touched. Distant parts of the cell also co-operate, so that the influence of the stimulus is not local only, but in consequence of it a change is brought about in other parts, arousing them. This property of transmitting disturbances is known as *conductivity*.

Finally, the movements excited are not, as a rule, random. They are not irregular convulsions, but are adapted to attain a certain end, being so combined as to bring the external particle into the interior of the cell. This capacity of all the parts to work together in definite strength and sequence to fulfil some purpose, is known as *co-ordination*.

These Properties Characteristic but not Diagnostic. These four faculties, irritability, conductivity, contractility and co-ordination, are possessed in a high degree by our Bodies as a whole. If the inside of the nose be tickled with a feather, a sneeze will result. Here the feather-touch (*stimulus*) has called forth movements which are mechanically altogether disproportionate to the energy of the contact, so that the living Body is clearly *irritable*. The movements, which are themselves a manifestation of *contractility*, are not exhibited at the point touched, but at more or less distant parts, among which those of abdomen, chest and face are visible from the exterior ; our Bodies therefore possess *physiological conductivity*. And finally these movements are not random, but combined so as to produce a violent current of air through the nose tending to remove the irritating object; and in this we have a manifestation of *co-ordination*. Speaking broadly, these properties are more manifest in animals than in plants, though they are by no means absolutely confined to the former. In the sensitive plant touching one leaflet will excite regular movements of the whole leaf, and many of

the lower aquatic plants exhibit movements as active as those of animals. On the other hand, no one of these four faculties is absolutely distinctive of living things in the way that *growth by intussusception* and *reproduction* are. Irritability is but a name for unstable molecular equilibrium, and is as marked in nitroglycerin as in any living cells; in the telephone the influence of the voice is conducted as a molecular change along a wire, and produces results at a distance; and many inanimate machines afford examples of the co-ordination of movements for the attainment of definite ends.

Spontaneity. There is, however, one character belonging to many of the movements exhibited by amœboid cells, in which they appear at first sight to differ fundamentally from the movements of inanimate objects. This character is their apparent *spontaneity* or *automaticity*. The cells frequently change their form independently of any recognizable external cause, while a dead mass at rest and unacted on from outside remains at rest. This difference is, however, only apparent and depends not upon any faculty of spontaneous action peculiar to the living cell, but upon its nutritive powers. It can be proved that any system of material particles in equilibrium and at rest will forever remain so if not acted upon by an external force. Such a system can carry on, under certain conditions, a series of changes when once a start has been given; but it cannot initiate them. Each living cell in the long-run is but a complex aggregate of molecules, composed in their turn of chemical elements, and if we suppose this whole set of atoms at rest in equilibrium at any moment, no change can be started in the cell from inside; in other words, it will possess no real spontaneity. When, however, we consider the irritability of amœboid cells, or, expressed in mechanical terms, the unstable equilibrium of their particles, it becomes obvious that a very slight external cause, such as may entirely elude our observation, may serve to set going in them a very marked series of changes, just as pressing the trigger will fire off a gun. Once the equilibrium of the cell has been disturbed, movements either of some of its constituent molecules or of its whole mass will continue until all the molecules have again settled down into a stable state. But in living cells the reattainment of this state is commonly indefinitely postponed by the reception of new particles, food in one form or another, from the exterior. The nearest ap-

proach to it is probably exhibited by the resting state into which some of the lower animals, as the wheel-animalcules, pass when dried slowly at a low temperature; the drying acting by checking the nutritive processes, which would otherwise have prevented the reattainment of molecular equilibrium. All signs of movement or other change disappear under these circumstances, but as soon as water again soaks into their substance and disturbs the existing condition, then the so-called " spontaneous" movements recommence. If, therefore, we use the term spontaneity to express a power in a resting system of particles of initiating changes in itself, it is possessed neither by living nor not-living things. But if we simply employ it to designate changes whose primary cause we do not recognize, and whose cause was in many cases long antecedent to the changes which we see, then the term is unobjectionable and convenient, as it serves to express briefly a phenomenon presented by many living things and finding its highest manifestation in many human actions. It then, however, no longer designates a property peculiar to them. A steam-engine with its furnace lighted and water in its boiler may be set in motion by opening a valve, and the movements thus started will continue spontaneously, in the above sense, until the coals or water are used up. The difference between it and the living cell lies not in any spontaneity of the latter, but in its nutritive powers, which enable it to replace continually what answers to the coals and water of the engine.

Protoplasm. The cell-body was formerly regarded as essentially made up of a single substance, which was named *protoplasm :* and now that its structure is known to be complex the term is retained as a convenient one for that mixture of spongioplasm and hyaloplasm which constitutes the main bulk of the bodies of most cells. With the protoplasm other things are frequently present, the most important of which are either materials undergoing anabolic changes but not yet completely built up into protoplasm, or katabolic materials resulting from the chemical degradation of protoplasm : these secondary matters, mingled with the completed protoplasm, are conveniently spoken of as the cell *deutoplasm* or *paraplasm.* As between the spongioplasm and hyaloplasm there are still some differences of opinion as to which is the more immediate agent in the manifestation of the vital activ-

ities of the cell. So far as the manifestation of the power of movement is concerned the evidence seems in favor of the hyaloplasm: the outermost parts of a white blood-corpuscle, for example, exhibit active contractile power, yet they contain no spongioplastic filaments; and many unicellular living things are known in which no reticular structure can be discovered and which nevertheless nourish themselves and are reproductive, irritable, contractile, conductive, co-ordinative and automatic. It is therefore possible that the filaments when present are to be regarded as secondary in importance to the hyaloplasm, partly serving as a mechanical support; but in addition they may play an important part in the internal economy of the cell. The study of the physiology of individual cells presents very great difficulties and is yet in its beginnings, so that we can do little more than speak of the properties of the cell as a whole, though from the frequent radial arrangement of the cell-protoplasm in its neighborhood and from the part it plays in the initiation of cell division, the attraction-particle appears to have a very important rôle.

Of the actual chemical composition of living matter we know only that its molecule is one of great complexity: all methods of chemical analysis break it up and alter it fundamentally, so that what is really analyzed is not living matter but a mixture of the products of its decomposition, among which proteid substances are always prominent.

Cell protoplasm no doubt varies a little in different cells, so that the name is to be regarded as a general term designating a number of closely-allied substances agreeing with one another chemically in main points, as the proteids do, but differing in minor details, in consequence of which one cell differs from another in faculty. On proximate analysis every mass of protoplasm is found to contain much water and a certain amount of mineral salts; the water being in part *constituent* or entering into the structure of the particles of protoplasm, and in part probably deposited in layers between them. Of organic constituents protoplasm always yields one or more proteids, some fats, and some starchy or saccharine body. So that the original protoplasm is probably to be regarded as containing chemical "residues" of proteids, fats and carbohydrates, combined with salts and water.

The name *nuclein* has been given to a substance or mixture of substances which are left behind when the cell-proto-

plasm has been dissolved away by various reagents: it contains a considerable quantity of phosphorus. In the living nucleus nuclein seems to be combined with various proteids to form *nucleo-albumins.*

The Fundamental Physiological Properties. All living animals possess in greater or less degree the properties considered in this chapter; and since the science of physiology is virtually concerned with considering how these properties are acquired, maintained and manifested, and for what ends they are employed, we may call them the *fundamental physiological properties.*

CHAPTER III.

THE DIFFERENTIATION OF THE TISSUES AND THE PHYSIOLOGICAL DIVISION OF EMPLOYMENTS.

Development. Every Human Body commences its individual existence as a single nucleated cell. This cell, known as the *ovum*, divides or *segments* and gives rise to a mass con-
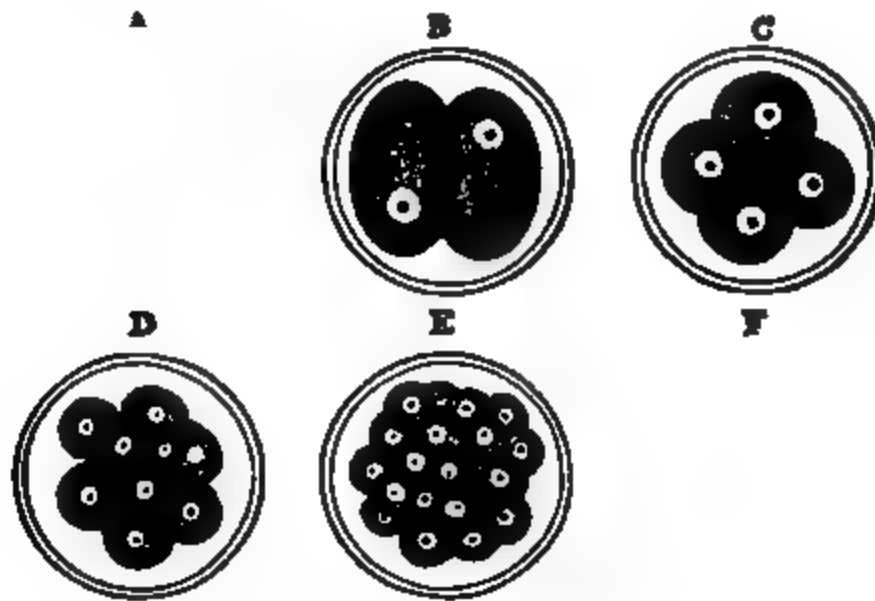
FIG. 11A.—*A*, an ovum; *B* to *E*, successive stages in its segmentation until the morula, *F*, is produced; *a*, cell-sac; *b*, cell contents; *c*, nucleus.

sisting of a number of similar units and called the *mulberry mass* or the *morula*. At this stage, long before birth, there are no distinguishable tissues entering into the structure of the Body, nor are any organs recognizable.

For a short time the morula increases in size by the growth and division of its cells, but very soon new processes occur which ultimately give rise to the complex adult body with its many tissues and organs. Groups of cells ceasing to grow and multiply like their parents begin to grow in ways peculiar to themselves, and so come to differ both from the original cells of the morula and from the cells of other groups, and this unlikeness becoming more and more marked, a varied whole is finally built up from one originally alike in

all its parts. Peculiar growth of this kind, forming a complex from a simple whole, is called *development;* and the process itself in this case is known as the *differentiation of the tissues,* since by it they are, so to speak, separated or specialized from the general mass of mother-cells forming the morula.

As the differences in the form and structure of the constituent cells of the morula become marked, differences in property arise, and it becomes obvious that the whole cell-aggregate is not destined to give rise to a collection of independent living things, but to form a single human being, in whom each part, while maintaining its own life, shall have duties to perform for the good of the whole. In other words, a single *compound individual* is to be built up by the union and co-operation of a number of simple ones represented by the various cells, each of which thenceforth, while primarily looking after its own interests and having its own peculiar faculties, has at the same time its activities subordinated to the good of the entire community.

The Physiological Division of Labor. The fundamental physiological properties, originally exhibited by all the cells, become ultimately distributed between the different modified cells which form the tissues of the fully developed Body much in the same way as different employments are distributed in a civilized state; for the difference between the fully developed Human Body and the collection of amoeboid cells from which it started is essentially the same as that between a number of wandering savages and a civilized nation. In the former, apart from differences dependent on sex, each individual has no one special occupation different from that of the rest, but has all his own needs to look after: he must collect his own food and prepare it for eating, make his own clothes, if he wear any, provide his own shelter, and defend himself from wild beasts or his fellow men. In the civilized country, on the other hand, we find agriculturists to raise food and cooks to prepare it, tailors to make clothes, and policemen and soldiers to provide protection. And just as we find that when distribution of employments in it is more minute a nation is more advanced in civilization, so is an animal higher or lower in the scale according to the degree in which it exhibits a division of physiological duties between its different tissues.

From the subdivision of labor in advanced communities several important consequences arise. In the first place, each man devoting himself to one kind of work mainly and relying upon others for the supply of his other needs, every sort of work is better done. The man who is constantly making boots becomes more expert than one whose attention is constantly distracted by other duties, and he can not only make more boots in a given time, but better ones; and so with the performance of all other kinds of work. In the second place, a necessity arises for a new sort of industry, in order to convey the produce of one individual in excess of the needs of himself and his family to those at a distance who may want it, and to convey back in return the excess of their produce which he needs. The carriage of food from the country to cities, and of city produce to country districts, and the occupation of shopkeeping, are instances of these new kinds of labor which arise in civilized communities. In addition there is developed a need for arrangements by which the work of individuals shall be regulated in proportion to the wants of the whole community, such as is in part effected by the agency of large employers of labor who regulate the activities of a number of individuals for the production of various articles in the different quantities required at different times.

Exactly similar phenomena result from the subdivision of labor in the Human Body. By the distribution of employments between its different tissues, each one specially doing one work for the general community and relying on the others for their aid in turn, every necessary work is better performed. And a need arises for a distributive mechanism by which the excess products, if any, of various tissues shall be carried to others which require them, and for a regulative mechanism by which the activities of the various tissues shall be rendered proportionate to the needs of the whole Body at different times and under different circumstances.

Classification of the Tissues.—As we might separate the inhabitants of the United States into groups, such as lawyers, doctors, clergymen, merchants, farmers, and so forth, so we may classify the tissues by selecting the most distinctive properties of each of those entering into the construction of the adult Body and arranging them into physiological groups; those of each group being characterized by some one prominent employment. No such classification, however, can be

more than approximately accurate, since the same tissue has often more than one well-marked physiological property. The following arrangement, however, is practically convenient.

1. UNDIFFERENTIATED TISSUES. These are composed of cells which have developed along no one special line, but retain very much the form and properties of the cells forming the very young Body before different tissues were recognizable in it. The lymph-corpuscles and the colorless corpuscles of the blood belong to this class.

2. SUPPORTING TISSUES. Including *cartilage* (gristle), *bone* and *connective tissue.* Of the latter there are several subsidiary varieties, the two more important being *white fibrous connective tissue,* composed mainly of colorless inextensible fibres, and *yellow fibrous tissue,* composed mainly of yellow elastic fibres. All the supporting tissues are used in the Body for mechanical purposes : the bones and cartilages form the hard framework by which softer tissues are supported and protected; and the connective tissues unite the various bones and cartilages, form investing membranes around different organs, and in the form of fine networks penetrate their substance and support their constituent cells. The functions of these tissues being for the most part to passively resist strain or pressure, none of them has any very marked physiological property; they are not, for example, irritable or contractile, and their mass is chiefly made up of an intercellular substance which has been formed by the actively living cells sparsely scattered through them, as for instance in cartilage, Fig. 45, where the cells are seen imbedded in cavities in a matrix which they have formed around them; and this matrix by its firmness and elasticity forms the functionally important part of the tissue.

3. NUTRITIVE TISSUES. These form a large group, the members of which fall into three main divisions, viz. :

Assimilative tissues, concerned in receiving and preparing food materials, and including—(*a*) *Secretory tissues,* composed of cells which make the digestive liquids poured into the alimentary canal and used to bring about chemical or other changes in the food. (*b*) *Receptive tissues,* represented by cells which line parts of the alimentary canal and take up the digested food.

Eliminative or *excretory tissues,* represented by cells in the

kidneys, skin, and elsewhere, whose main business it is to get rid of the waste products of the various parts of the Body.

Respiratory tissues. These are concerned in the gaseous interchanges between the Body and the surrounding air. They are constituted by the cells lining the lungs and by the colored corpuscles of the blood.

As regards the nutritive tissues it requires especially to be borne in mind that although such a classification as is here given is useful, as helping to show the method pursued in the domestic economy of the Body, it is only imperfect and largely artificial. Every cell of the Body is in itself assimilative, respiratory, and excretory, and the tissues in this class are only those concerned in the first and last interchanges of material between it and the external world. They provide or get rid of substances for the whole Body, leaving the feeding and breathing and excretion of its individual tissues to be ultimately looked after by themselves, just as even the mandarin described by Robinson Crusoe who found his dignity promoted by having servants to put the food into his mouth, had finally to swallow and digest it for himself. Moreover, there is no logical distinction between a secretory and an excretory cell: each of them is characterized by the separation of certain substances which are poured out on a free surface on the exterior or interior of the Body. Many secretory cells too. have no concern with the digestion of food, as for example those which form the tears and sweat.

4. STORAGE TISSUES. The Body does not live from hand to mouth: it has always in health a supply of food-materials accumulated in it beyond its immediate needs. This lies in part in the individual cells themselves, just as in a prosperous community nearly every one will have some little pocket-money. But apart from this reserve there are certain cells, a sort of capitalists, which store up considerable quantities of material and constitute what we will call the *storage tissues.* These are especially represented by the liver-cells and fat-cells, which contain in health a reserve fund for the rest of the Body. Since both of these, together with secretory and excretory cells, are the seats of great chemical changes, they are all often called *metabolic tissues.*

5. IRRITABLE TISSUES. The maintenance, or at any rate the best prosperity, of a nation is not fully secured when a division of labor has taken place in food-supply and food-dis-

tribution employments. It is extremely desirable that means shall be provided by which it may receive information of external changes which may affect it as a whole, such as the policy of foreign countries; or which shall enable the inhabitants of one part to know the needs of another, and direct their activity accordingly. Foreign ministers and consuls and newspaper correspondents are employed to place it in communication with other states and keep it informed as to its interests; and we find also organizations, such as the meteorological department, to warn distant parts of approaching storms or other climatic changes which may seriously affect the pursuits carried on in them. In the Human Body we have a comparable class of intelligence-gaining tissues lying in the sense-organs, whose business it is to obtain and communicate to the whole information of external changes which occur around it. Since the usefulness of these tissues depends upon the readiness with which slight causes excite them to activity, we may call them the *irritable tissues*.

6. Co-ordinating and Automatic Tissues. Such information as that collected by ministers in foreign parts or by meteorological observers is usually sent direct to some central office from which it is redistributed; this mere redistribution is, however, in many cases but a small part of the work carried on in such offices. Let us suppose information to be obtained that an Indian chief is collecting his men for an attack on some point. The news is probably first transmitted to Washington, and it becomes the duty of the executive officers there to employ certain of the constituent units of the nation in such definite work as is needed for its protection. Troops have to be sent to the place threatened perhaps; recruits enlisted; food and clothes, weapons and ammunition, must be provided for the army; and so on. In other words, the work of the various classes composing the society has to be organized for the common good: the mere spreading the news of the danger would be of little avail. So in the Body: the information forwarded to certain centres from the irritable tissues is used in such a way as to arouse to orderly activity other tissues whose services are required; we find thus in these centres a group of *co-ordinating tissues*, represented by *nerve-cells* and possibly by certain other constituents of the nerve-centres. Certain nerve-cells are also *automatic* in the physiological sense already pointed

out. The highest manifestation of this latter faculty, shown objectively by muscular movements, is subjectively known as the " will," a state of consciousness; and other mental phenomena, as sensations and emotions, are also associated with the activity of nerve-cells lying in the brain. How it is that any one state of a material cell should give rise to a particular state of consciousness is a matter quite beyond our powers of conception; but not really more so than how it is that every portion of matter attracts every other portion according to the law of gravitation. In the living Body, as elsewhere in the universe, we can study phenomena and make out their relations of sequence or coexistence; but why one phenomenon is accompanied by another, why in fact any cause produces an effect, is a matter quite beyond our reach in every case; whether it be a sensation accompanying a molecular change in a nerve-cell, or the fall of a stone to the ground in obedience to the force of gravity.

7. MOTOR TISSUES. These have the contractility of the original protoplasmic masses highly developed. The more important are *ciliated cells* and *muscular tissue.* The former line certain surfaces of the body, and possess on their free surfaces fine threads which are in constant movement. One finds such cells, for example (Fig. 50), lining the inside of the windpipe, where their threads or *cilia* serve, by their motion, to sweep any fluid formed there towards the throat, where it can be coughed up and got rid of. Muscular tissue occurs in two main varieties. One kind is found in the muscles attached to the bones, and is that used in the ordinary voluntary movements of the Body. It is composed of fibres which present cross-stripes when viewed under the microscope (Fig. 56), and is hence known as *striped* or *striated muscular tissue.* The other kind of muscular tissue is found in the walls of the alimentary canal and some other hollow organs, and consists of clongated cells (Fig. 60) which present no cross-striation. It is known as *plain* or *unstriated muscular tissue.*

The cells enumerated under the heading of " undifferentiated tissues " might also be included among the motor tissues, since they are capable of changing their form.

8. THE CONDUCTIVE TISSUES. These are represented by the *nerve-fibres,* slender threads, each of which has as its essential part a branch of a nerve-cell having the property of physiological conductivity highly developed; the fibres therefore

readily transmit molecular disturbances. When its equilib-
rium is upset at one end, a nerve-fibre transmits to its other
end a molecular movement known as a *"nervous impulse,"*
and so can excite parts distant from the original exciting
force. Nerve-fibres place, on the one hand, the irritable
tissues in connection with the automatic, co-ordinating, and
sensory; and on the other put the three latter in communica-
tion with the muscular, secretory and other tissues.

9. PROTECTIVE TISSUES. These consist of certain cells lin-
ing cavities inside the body and called *epithelial cells*, and cells
covering the whole exterior of the Body and forming *epider-
mis, hairs* and *nails*. The *enamel* which
covers the teeth belongs also to this
group.

The class of protective tissues is, how-
ever, even more artificial than that of the
nutritive tissues, and cannot be defined by
positive characters. Many epithelial cells
are secretory, excretory or receptive; and
ciliated cells have already been included
among the motor tissues, although from
the fact that the movements of their cilia
go on in separated cells and independently
of recognizable external stimuli, they
might well have been put among the automatic. The protec-
tive tissues may be best defined as including cells which cover
free surfaces, and whose functions are mainly mechanical or
physical. In their simplest form epithelial cells are flat
scales, as, for example, those represented in Fig. 11B, from
the lining membrane of the abdominal cavity.

FIG. 11B. — Flat epithe-
lium cells from the sur-
face of the peritoneum.
a, cell-body; *c*, nucleus;
b, nucleoli.

10. THE REPRODUCTIVE TISSUES. These are concerned in
the production of new individuals, and in the Human Body
are of two kinds, located in different sexes. The conjunction
of the products of each sex is necessary for the origination
of offspring, since the female product, egg-cell or ovum,
which directly develops into the new human being, remains
dormant until it has been *fertilized*, and fertilization consists
essentially in the fusion of its nucleus with the nucleus of a
cell produced by the male.

The Combination of Tissues to Form Organs. The va-
rious tissues above enumerated forming the building materials
of the Body, anatomy is primarily concerned with their struc-

ture, and physiology with their properties. If this, however, were the whole matter, the problems of anatomy and physiology would be much simpler than they actually are. The knowledge about the living Body obtained by studying only the forms and functions of the individual tissues would be comparable to that attained about a great factory by studying separately the boilers, pistons, levers, wheels, etc., found in it, and leaving out of account altogether the way in which these are combined to form various machines; for in the Body the various tissues are for the most part associated to form *organs*, each organ answering to a complex machine like a steam-engine with its numerous constituent parts. And just as in different machines a cogged wheel may perform very different duties, dependent upon the way in which it is connected with other parts, so in the Body any one tissue, although its essential properties are everywhere the same, may by its activity subserve very various uses according to the manner in which it is combined with others. For example: A nerve-fibre uniting the eye with one part of the brain will, by means of its conductivity, when its end in the eye is excited by the irritable tissue attached to it on which light acts, cause changes in the sensory nerve-cells connected with its other end and so arouse a sight sensation; but an exactly similar nerve-fibre running from the brain to the muscles will, also by virtue of its conductivity, when its ending in the brain is excited by a change in a nerve-cell connected with it, stir up the muscle to contract under the control of the will. The different results depend on the different parts connected with the ends of the nerve-fibres in each case, and not on differences in the properties of the nerve-fibres themselves.

It becomes necessary then to study the arrangement and uses of the tissues as combined to form various organs, and this is frequently far more difficult than to make out the structure and properties of the individual tissues. An ordinary muscle, such as one sees in the lean of meat, is a very complex organ, containing not only contractile muscular tissue, but supporting and uniting connective tissue and conductive nerve-fibres, and in addition a complex commissariat arrangement, composed in its turn of several tissues, concerned in the food-supply and waste removal of the whole muscle. The anatomical study of a muscle has to take into

account the arrangement of all these parts within it, and also its connections with other organs of the Body. The physiology of any muscle must take into account the actions of all these parts working together and not merely the functions of the muscular fibres themselves, and has also to make out under what conditions the muscle is excited to activity by changes in other organs, and what c'.anges in these it brings about when it works.

Physiological Mechanisms. Even the study of organs added to that of the separate tissues does not exhaust the matter. In a factory we frequently find machines arranged so that two or more shall work together for the performance of some one work: a steam-engine and a loom may, for example, be connected and used together to weave carpets. Similarly in the Body several organs are often arranged to work together so as to attain some one end by their united actions. Such combinations are known as *physiological apparatuses*. The circulatory apparatus, for example, consists of various organs (each in turn composed of several tissues) known as heart, arteries, capillaries and veins. The *heart* forms a force-pump by which the blood is kept flowing through the whole mechanism, and the rest, known together as the *blood-vessels*, distribute the blood to the various organs and regulate the supply according to their needs. Again, in the visual apparatus we find the co-operation of (*a*) a set of optical instruments which bring the light proceeding from external objects to a focus upon (*b*) the *retina*, which contains highly irritable parts; these, changed by the light, stimulate (*c*) the *optic nerve*, which is conductive and transmits a disturbance which arouses in turn (*d*) sensory parts in the *brain*. In the production of ordinary sight sensations all these parts are concerned and work together as a visual apparatus. So, too, we find a *respiratory apparatus*, consisting primarily of two hollow organs, the *lungs*, which lie in the chest and communicate by the *windpipe* with the back of the throat, from which air enters them. But to complete the respiratory apparatus are many other organs, bones, muscles, nerves and nerve-centres, which work together to renew the air in the lungs from time to time; and the act of breathing is the final result of the activity of the whole apparatus.

Many similar instances, as the alimentary apparatus, the

auditory apparatus, and so on, will readily be thought of. The study of the working of such complicated mechanisms forms a very important part of physiology.

Anatomical Systems. From the anatomical side a whole collection of bodily organs agreeing in structure with one another is often spoken of as a system; all the muscles, for example, are grouped together as the *muscular system*, and all the bones as the *osseous system*, and so on, without any reference to the different uses of different muscles or bones. The term system is, however, often used as equivalent to " apparatus ": one reads indifferently of the " circulatory system " or the " circulatory apparatus." It is better, however, to reserve the term system for a collection of organs classed together on account of similarity of structure; and " apparatus " for a collection of organs considered together on account of their co-operation to execute one function. The former term will then have an anatomical, the latter a physiological, significance.

The Body as a Working Whole. Finally it must all through be borne in mind that not even the most complex system or apparatus can be considered altogether alone as an independently living part. All are united to make one living Body, in which there is throughout a mutual interdependence, so that the whole forms one human being, in whom the circulatory, respiratory, digestive, sensory and other apparatuses are constantly influencing one another, each modifying the activities of the rest. This interaction is mainly brought about through the conductive and co-ordinating tissues of the nervous system, which place all parts of the Body in communication. But in addition to this another bond of union is formed by the blood, which by the circulatory apparatus is carried from tissue to tissue and organ to organ and so, bringing materials derived in one region to distant parts, enables each organ to influence all the rest for good or ill.

Besides the blood another liquid, called *lymph*, exists in the Body. It is contained in vessels distinct from those which carry the blood, but emptying into the blood-vessels at certain points. This liquid being also in constant movement forms another agency by which products are carried from part to part, and the welfare or ill-fare of one member enabled to influence all.

CHAPTER IV.

THE INTERNAL MEDIUM.

The External Medium. During the whole of life interchanges of material go on between every living being and the external world; by these exchanges material particles that one time constitute parts of inanimate objects come at another to form part of a living being; and later on these same atoms, after having been a part of a living thing, are passed out from it in the form of lifeless compounds. As the foods and wastes of various organisms differ more or less, so are more or less different environments suited for their existence; and there is accordingly a relationship between the plants and animals living in any one place and the conditions of air, earth and water prevailing there. Even such simple unicellular animals as the amœbæ live only in water or mud containing in solution certain gases, and in suspension solid food-particles; and they soon die if the water be changed either by essentially altering its gases or by taking out of it the solid food. So in yeast we find a unicellular plant which thrives and multiplies only in liquids of certain composition, and which in the absence of organic compounds of carbon in solution will not grow at all. Each of these simple living things, which corresponds to one only of the innumerable cells composing the full-grown Human Body, thus requires for the manifestation of its vital properties the presence of a surrounding medium suited to itself: the yeast would die, or at the best lie dormant, in a liquid containing only the solid organic particles on which the amœba lives; and the amœba would die in such solutions as those in which yeast thrives best.

The Internal Medium. A similar close relationship between the living being and its environment, and an interchange between the two like that which we find in the amœba and the yeast-cell, we find also in even the most complex living beings. When, however, an animal comes to be com-

posed of many cells, some of which are placed far away from the surface of its body and from immediate contact with the environment, there arises a new need—a necessity for an internal medium or *plasma* which shall play the same part toward the individual cells as the surrounding air, water and food to the whole animal. This internal medium kept in movement and receiving at some regions of the bodily surfaces materials from the exterior, while losing substances to the exterior at the same or other surfaces, forms a sort of middleman between the individual tissues and the surrounding world, and stands in the same relationship to each of the cells of the Body as the water in which an amœba lives does to that animal, or beer-wort does to a yeast-cell. We find accordingly the Human Body pervaded by a liquid plasma, containing gases and food-material in solution, the presence of which is necessary for the maintenance of the life of the tissues. Any great change in this medium will affect injuriously few or many of the groups of cells in the Body, or may even cause their death; just as altering the media in which they live will kill an amœba or a yeast-cell.

The Blood. In the Human Body the internal medium is primarily furnished by the *blood*, which, as every one knows, is a red liquid very widely distributed over the frame, since it flows from any part when the skin is cut through. There are in fact very few portions of the Body into which the blood is not carried. One of the exceptions is the epidermis or outer layer of the skin: if a cut be made through it only, leaving the deeper skin-layers intact, no blood will flow from the wound. Hairs and nails also contain no blood. In the interior of the Body the epithelial layers lining free surfaces, such as the inside of the alimentary canal, contain no blood, nor do the hard parts of the teeth, the cartilages, and the refracting media of the eye (see Chap. XXXII), but these interior parts are moistened with liquid of some kind, and unlike the epidermis are protected from rapid evaporation. All these bloodless parts together form a group of *non-vascular tissues;* they alone excepted, a wound of any part of the Body will cause bleeding.

In many of the lower animals there is no need that the liquid representing their blood should be renewed very rapidly in different parts. Their cells live slowly, and so require but little food and produce but little waste. In a sea-anemone,

for example, there is no special arrangement to keep the blood moving; it is just pushed about from part to part by the general movements of the body of the animal. But in higher animals, especially those with an elevated temperature, such an arrangement, or rather absence of arrangement, as this would not suffice. In them the constituent cells live very fast, making much waste and using much food, and altering the blood in their neighborhood very rapidly. Besides, we have seen that in complex animals certain cells are set apart to get food for the whole organism and certain others to finally remove its wastes, and there must be a sure and rapid interchange of material between the feeding and excreting tissues and all the others. This can only be brought about by a rapid movement of the blood in a definite course, and that is accomplished by shutting it up in a closed set of tubes, and placing somewhere a pump, which constantly takes in blood from one end of the system of tubes and forces it out again into the other. Sent by this pump, the *heart*, through all parts of the Body and back to the heart again, the blood gets food from the receptive cells, takes it to the working cells, carries off the waste of these latter to the excreting cells; and so the round goes on.

The Lymph. The blood, however, lies everywhere in closed tubes formed by the vascular system, and does not come into direct contact with any cells of the Body except those which float in it and those which line the interior of the
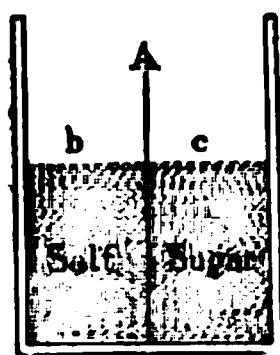
Fig. 12.—A diagram of a dialyzing apparatus, containing two liquids, b and c, separated by a moist animal membrane.

blood-vessels. At one part of its course, however, the vessels through which it passes have extremely thin coats, and through the walls of these *capillaries* liquid transudes from the blood and bathes the various tissues. The transuded liquid is the *lymph*, and it is this which forms the immediate nutrient plasma of the tissues except the few which the blood moistens directly.

Dialysis. When two liquids containing different matters in solution are separated from one another by a moist animal membrane, an interchange of material will take place under certain conditions. If *A* be a vessel (Fig. 12) completely divided vertically by such a membrane, and a solution of common salt in water be placed on the side *b*, and a solution of sugar in water on the side *c*, it

will be found after a time that some salt has got into *c* and some sugar into *b*, although there are no visible pores in the partition. Such an interchange is said to be due to *dialysis* or *osmosis*, and if the process were allowed to go on for some hours the same proportions of salt and sugar would be found in the solution on either side of the dividing membrane.

The Renewal of the Lymph. Osmotic phenomena play a great part in the nutritive processes of the Body. The lymph present in any organ gives up things to the cells there and gets things from them; and thus, although it may have originally been tolerably like the liquid part of the blood, it soon acquires a different chemical composition. Diffusion or dialysis then commences between the lymph outside and the blood inside the capillaries, and the latter gives up to the lymph new materials in place of those which it has lost and takes from it the waste products it has received from the tissues. When this blood, altered by exchanges with the lymph, gets again to the neighborhood of the receptive cells, having lost some food-materials it is poorer in these than the richly supplied lymph around those cells, and takes up a supply by dialysis from it. When it reaches the excretory organs it has previously picked up a quantity of waste matters and loses these by dialysis to the lymph there present, which is specially poor in such matters, since the excretory cells constantly deprive it of them. In consequence of the different wants and wastes of various cells, and of the same cells at different times, the lymph must vary considerably in composition in various organs of the Body, and the blood flowing through them will gain or lose different things in different places. But renewing during its circuit in one what it loses in another, its average composition is kept pretty constant, and, through interchange with it, the average composition of the lymph also.

The Lymphatic Vessels. The blood, on the whole, loses more liquid to the lymph through the capillary walls than it receives back the same way. This depends mainly on the fact that the pressure on the blood inside the vessels is greater than that on the lymph outside, and so a certain amount of filtration of liquid from within out occurs through the vascular wall in addition to the dialysis proper. The excess is collected from the various organs of the Body into a set of *lymphatic vessels* which carry it directly back into some of

the larger blood-vessels near where these empty into the heart; by this flow of the lymph, under pressure from behind, it is renewed in various organs, fresh liquid filtering through the capillaries to take its place as fast as the old is carried off.

The Lacteals. In the walls of the alimentary canal certain food-materials after passing through the receptive cells into the lymph are not transferred locally, like the rest, by dialysis into the blood, but are carried off bodily in the lymph-vessels and poured into the veins of a distant part of the Body. The lymphatic vessels concerned in this work, being frequently filled with a white liquid during digestion, are called the *milky* or *lacteal vessels.*

Summary. To sum up: the blood and lymph form the internal medium in which the tissues of the Body live; the lymph is primarily derived from the blood and forms the immediate plasma for the great majority of the living cells of the Body; and the excess of it is finally returned to the blood. The lymph moves but slowly, but is constantly renovated by the blood, which is kept in rapid movement, and which, besides containing a store of new food-matters for the lymph, carries off the wastes which the various cells have poured into the latter, and thus is also a sort of sewage stream into which the wastes of the whole Body are primarily collected.

Microscopic Characters of Blood. If a finger be pricked, and the drop of blood flowing out be spread on a glass slide, covered, protected from evaporation, and examined with a microscope magnifying about 400 diameters, it will be seen to consist of innumerable solid bodies floating in a liquid. The solid bodies are the *blood-corpuscles,* and the liquid is the *blood-plasma* or *liquor sanguinis.*

The corpuscles are not all alike. While currents still exist in the freshly-spread drop of blood, the great majority of them are readily carried to and fro; but a certain number more commonly stick to the glass and remain in one place. The former are the *red,* the latter the *pale* or *colorless blood-corpuscles.*

Red Corpuscles. *Form and Size.* The red corpuscles as they float about frequently seem to vary in form, but by a little attention it can be made out that this appearance is due to their turning round as they float, and so presenting different aspects to view; just as a silver dollar presents a different

outline according as it is looked at from the front or edge-wise or in three-quarter profile.

Sometimes the corpuscle (Fig. 13, *B*) appears circular; then it is seen in full face; sometimes linear (*C*), and slightly narrowed in the middle; sometimes oval, as the dollar when half-way between a full and a side view. These appearances show that each red corpuscle is a circular disk, slightly hollowed in the middle (or biconcave) and about four times as wide as it is thick. The average transverse diameter is 0.008 milimeter ($\frac{1}{3155}$ inch). Shortly after blood is drawn the
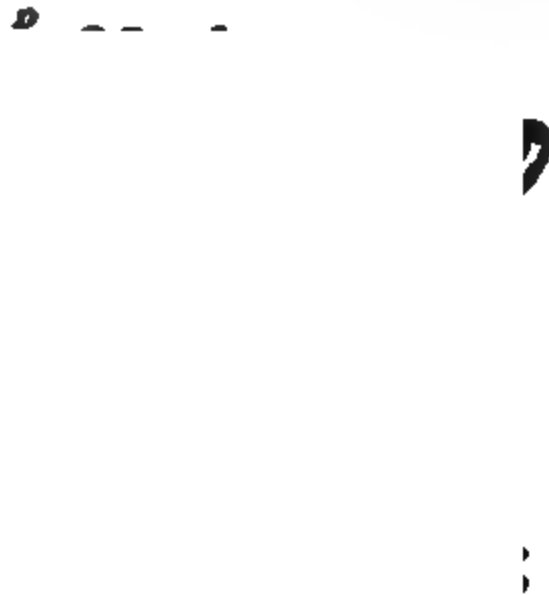
corpuscles arrange themselves in rows, or *rouleaux*, adhering to one another by their broader surfaces.

Color.—Seen singly each red corpuscle is of a pale yellow color; it is only when collected in masses that they appear red. The blood owes its red color to the great numbers of these bodies in it; if it is spread out in a very thin layer it, too, is yellow. In a cubic millimeter ($\frac{1}{17}$ inch) of blood there are about five million red corpuscles.

Structure.—Seen from the front the central part of each red corpuscle in a certain focus of the microscope appears dimmer or darker than the rest (Fig. 13, *B*), ex-

cept a narrow band near the outer rim. If the lens of the microscope be raised, however, this previously dimmer central part becomes brighter, and the previously brighter part obscure (*E*). This difference in appearance does not indicate the presence of a central part or *nucleus* different from the rest, but is an optical phenomenon due to the shape of the corpuscle, in consequence of which it acts like a little biconcave lens. Rays of light passing through near the centre of the corpuscles are refracted differently from those passing through elsewhere; and when the microscope is so focussed that the latter reach the eye, the former do not, and *vice versa ;* thus when the central parts look bright, those around them look obscure, and the contrary.

There is no satisfactory evidence that these corpuscles have any enveloping sac or cell-wall. All the methods used to bring one into view under the microscope are such as would coagulate the outer layers of the substance composing the corpuscle and so make an artificial envelope. So far as optical analysis goes, then, each corpuscle is homogeneous throughout. By other means we can, however, show that at least two materials enter into the structure of each red corpuscle. If the blood be diluted with several times its own bulk of water and examined with the microscope, it will be found that the formerly red corpuscles are now colorless and the plasma colored. The dilution has caused the coloring matter to pass out of the corpuscles and dissolve in the liquid. This coloring constituent of the corpuscle is *hæmoglobin,* and the colorless residue which it leaves behind and which swells up into a sphere in the diluted plasma is the *stroma.* In the living corpuscle the two are intimately mingled throughout it, and so long as this is the case the blood is opaque; but when the coloring matter dissolves in the plasma, then the blood becomes transparent, or, as it is called, *laky.* The difference may be very well seen by comparing a thin layer of fresh blood diluted with ten times its volume of ten-per-cent salt solution with a similar layer of blood diluted with ten volumes of water. The watery mixture is a dark transparent red; the other, in which the coloring matter still lies in the corpuscles, is a brighter opaque red.

Consistency.—Each red corpuscle is a soft jelly-like mass which can be readily crushed out of shape. Unless the pressure be such as to rupture it, the corpuscle immediately reas-

sumes its proper form when the external force is removed. The corpuscles are, then, highly elastic; they frequently can be seen much dragged out of shape inside the vessels when the circulation of the blood is watched in a living animal (Chap. XV), but immediately springing back to their normal form when they get a chance.

Blood-crystals. Hæmoglobin is, as above shown, readily soluble in water. In this it soon decomposes if kept in a warm room, breaking up into a colorless proteid substance called *globulin* and a red body, *hæmatin*. By keeping the hæmoglobin solution very cold, however, this decomposition can be greatly retarded, and at the same time the solubility of the hæmoglobin in the water much diminished. In dilute alcohol hæmoglobin is still less soluble, and so if its ice-cold watery solution have one fourth of its volume of cold alcohol added to it and the mixture be put in a refrigerator for twenty-four hours, a part of the hæmoglobin will often crystallize out and sink to the bottom of the vessel, where it can be collected for examination. The hæmo-
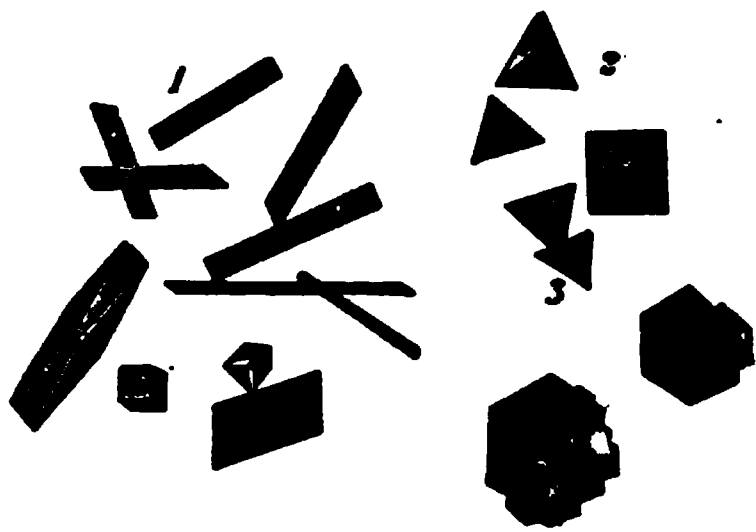
Fig. 14.—Blood-crystals, or hæmoglobin crystals.

globin of the rat is less soluble than that of man, and therefore crystallizes out especially easily; but these hæmoglobin crystals, or, as they are often called, *blood-crystals*, can also be obtained from human blood. In 100 parts of dry human red blood-corpuscles there are of 90 hæmoglobin. The hæmoglobin is the essential constituent of the red blood-corpuscles, enabling them to pick up large quantities of oxygen in the lungs and carry it to other parts. (See Respiration.)

Hæmoglobin contains a considerable quantity of iron, much more than any other proximate constituent of the Body.

The Colorless Blood-corpuscles (Fig. 13, *F, H, G*). The *colorless, pale* or *white corpuscles* of the blood are far less numerous than the red; in health there is on the average about one white to three hundred red, but the proportion may vary considerably Each is finely granular and consists of a soft mass of protoplasm enveloped in no definite cell-wall, but containing a nucleus. The granules in the protoplasm

commonly hide the nucleus in a fresh corpuscle, but dilute acetic acid dissolves most of them and brings the nucleus into view. These pale corpuscles belong to the group of undifferentiated tissues, and differ in no important recognizable character from the cells which make up the whole very young Human Body, nor indeed from such a unicellular animal as an Amœba. They have the power of slowly changing their form spontaneously. At one moment a pale corpuscle will be seen as a spheroidal mass; a few seconds later (Fig. 15) processes will be seen radiating from this, and soon after

Fig. 15.—A white blood-corpuscle sketched at successive intervals of a few seconds to illustrate the changes of form due to its amœboid movements.

these processes may be retracted and others thrust out; and so the corpuscle goes on changing its shape. These slow *amœboid movements* are greatly promoted by keeping the specimen of blood at the temperature of the Body. By thrusting out a process on one side, then drawing the rest of its body up to it, and then sending out a process again on the same side, the corpuscle can slowly change its place and creep across the field of the microscope. Inside the blood-vessels these corpuscles often execute similar movements; and they sometimes bore right through the capillary walls and, getting out into the lymph-spaces, creep about among the other tissues. This *migration* is especially frequent in inflamed parts, and the *pus* or *"matter"* which collects in abscesses is largely made up of white blood-corpuscles which have in this way got out of the blood-vessels. The average diameter of the white corpuscles is one third greater than that of the red.

The colorless corpuscles, or some of them, are capable of taking into themselves foreign particles present in the blood; this they do in a manner similar to that in which an amœba feeds: the process is known as *phagocytosis* and the cells exhibiting it as *phagocytes*. Among the substances observed to be taken up by white corpuscles are the minute organisms known as Bacteria, certain species of which have been proved to be the causes of some diseases (*zymotic diseases*). The white corpuscles may in this way play an important part in the cure of such diseases, or in their prevention in persons exposed to infection. The accumulation of white corpuscles in inflamed or injured parts is probably primarily as-

sociated with the removal of dead and broken-down tissues, though it may be carried to excess as in the case of purulent accumulations.

The Blood Platelets or Plaques are a third kind of blood-corpuscle, considerably smaller than the red, but somewhat resembling them in form. They adhere together, break down and form sticky clumps with great rapidity in drawn blood unless special precautions are taken.

Blood of Other Animals. In all animals with blood the pale corpuscles are pretty much alike, but the red corpuscles, which with rare exceptions are found only in Vertebrates, vary considerably. In all the classes of the mammalia they are circular biconcave disks, with the exception of the camel tribe, in which they are oval. They vary in diameter from 0.02 mm. ($\frac{1}{3100}$ inch) (musk deer) to .011 mm. ($\frac{1}{2470}$ inch) (elephant). In the dog they are nearly the same size as those of man. In no mammals do the fully-developed red corpuscles possess a nucleus. In all other vertebrate classes the red corpuscles possess a central nucleus, and are oval slightly biconvex disks, except in a few fishes in which they are circular. They are largest of all in the amphibia. Those of the frog are 0.02 mm. ($\frac{1}{1400}$ inch) long and .007 mm. ($\frac{1}{4000}$ inch) broad.

Histology of Lymph. Pure lymph is a colorless watery-looking liquid; examined with a microscope it is seen to contain numerous pale corpuscles closely resembling those of the blood, and no doubt many are pale blood-corpuscles which have migrated. These lymph-corpuscles or *leucocytes* have, however, another more important origin. In many parts of the Body there are collections of a peculiar *lymphoid* or *adenoid tissue*, sometimes in nodular masses (lymphatic glands). This tissue consists essentially of a fine network, the meshes of which are occupied with leucocytes which frequently show signs of division. The meshes of the network communicate with lymphatic vessels and the lymph flowing through picks up and carries off the new-formed leucocytes. The lymph being ultimately poured into the blood, the leucocytes become the colorless corpuscles of the latter; and the migrating cells of the blood are therefore but lymph-corpuscles restored to the lymph, perhaps somewhat changed during their life in the blood-plasma.

The lymph flowing from the intestines during digestion

is, as already mentioned, not colorless, but white and milky. It is known as *chyle,* and will be considered with the process of digestion. During fasting the lymph from the intestines is colorless, like that from other parts of the Body.

CHAPTER V.

THE CLOTTING OF BLOOD.

The Coagulation of the Blood. When blood is first drawn from the living Body it is perfectly liquid, flowing in any direction as readily as water. This condition is, however, only temporary; in a few minutes the blood becomes viscid and sticky, and the viscidity becomes more and more marked until, after the lapse of five or six minutes, the whole mass sets into a jelly which adheres to the vessel containing it, so that this may be inverted without any blood whatever being spilled. This stage is known as that of *gelatinization* and is also not permanent. In a few minutes the top of the jelly-like mass will be seen to be hollowed or "cupped" and in the concavity will be seen a small quantity of nearly colorless liquid, the *blood-serum*. The jelly next shrinks so as to pull itself loose from the sides and bottom of the vessel containing it, and as it shrinks squeezes out more and more serum. Ultimately we get a solid *clot*, colored red and smaller in size than the vessel in which the blood coagulated though retaining its form, floating in a quantity of pale yellow *serum*. If, however, the blood be not allowed to coagulate in perfect rest, a certain number of red corpuscles will be rubbed out of the clot into the serum and the latter will be more or less reddish. The longer the clot is kept the more serum will be obtained: if the first quantity exuded be decanted off and the clot put aside and protected from evaporation, it will in a short time be found to have shrunk to a smaller size and to have pressed out more serum; and this goes on until putrefactive changes commence.

Cause of Coagulation. If a drop of fresh-drawn blood be spread out very thin and watched for a few minutes with a microscope magnifying 600 or 700 diameters, it will be seen that the coagulation is due to the separation of very fine solid threads which run in every direction through the plasma and form a close network entangling all the corpuscles. These

threads are composed of the proteid substance *fibrin.* When they first form, the whole drop is much like a sponge soaked full of water (represented by the serum) and having solid bodies (the corpuscles) in its cavities. After the fibrin threads have been formed they tend to shorten; hence when blood clots in mass in a vessel, the fibrinous network tends to shrink in every direction just as a network formed of stretched india-rubber bands would, and this shrinkage is greater the longer the clotted blood is kept. At first the threads stick too firmly to the bottom and sides of the vessel to be pulled away, and thus the first sign of the contraction of the fibrin is seen in the cupping of the surface of the gelatinized blood where the threads have no solid attachment, and there the contracting mass presses out from its meshes the first drops of serum. Finally the contraction of the fibrin overcomes its adhesion to the vessel and the clot pulls itself loose on all sides, pressing out more and more serum, in which it ultimately floats. The great majority of the red corpuscles are held back in the meshes of the fibrin, but a good many pale corpuscles, by their amœboid movements, work their way out and get into the serum.

Whipped Blood. The essential point in coagulation being the formation of fibrin in the plasma, and blood only forming a certain amount of fibrin, if this be removed as fast as it forms the remaining blood will not clot. The fibrin may be separated by what is known as " whipping " the blood. For this purpose fresh-drawn blood is stirred up vigorously with a bunch of twigs, and to these the sticky fibrin threads as they form, adhere. If the twigs be withdrawn after a few minutes a quantity of stringy material will be found attached to them. This is at first colored red by adhering blood-corpuscles: but by washing in water they may be removed, and the pure fibrin thus obtained is perfectly white and in the form of highly elastic threads. It is insoluble in water and in dilute acids, but swells up to a transparent jelly in the latter. The " whipped " or " defibrinated blood " from which the fibrin has been in this way removed, looks just like ordinary blood, but has lost the power of coagulating spontaneously.

The Buffy Coat. That the red corpuscles are not an essential part of the clot, but are merely mechanically caught up in it, seems clear from the microscopic observation of the process of coagulation; and from the fact that perfectly

formed fibrin can be obtained free from corpuscles by whipping the blood and washing the threads which adhere to the twigs. Under certain conditions, moreover, one gets a naturally formed clot containing no red corpuscles in one part of it. The corpuscles of human blood are a little heavier, bulk for bulk, than the plasma in which they float; hence, when the blood is drawn and left at rest they sink slowly in it; and if for any reason clotting take place more slowly or the corpuscles sink more rapidly than usual, a colorless top stratum of plasma, with no red corpuscles in it, is left before gelatinization occurs and stops the further sinking of the corpuscles. The uppermost part of the clot formed under such circumstances is colorless or pale yellow, and is known as the *buffy coat;* it is especially apt to be formed in the blood drawn from febrile patients, and was therefore a point to which physicians paid much attention in the olden times when bloodletting was thought to be almost a panacea. In horse's blood the difference between the specific gravity of the corpuscles and that of the plasma is greater than in human blood, and horse's blood also coagulates more slowly, so that its clot has nearly always a buffy coat. The colorless buffy coat seen sometimes on the top of the clot must, however, not be confounded with another phenomenon. When a blood-clot is left floating exposed to the air its top becomes bright scarlet, while the part immersed in the serum assumes a dark purple-red color. The brightness of the top layer is due to the action of the oxygen of the air, which forms a scarlet compound with the coloring matter of the red corpuscles. If the clot be turned upside down and left for a short time, the previously dark red bottom layer, now exposed to the air, becomes bright; and the previously bright top layer, now immersed in the serum, loses its oxygen and becomes dark.

Uses of Coagulation. The clotting of the blood is so important a process that its cause has been frequently investigated; but it is not yet completely understood. The living circulating blood in the healthy blood-vessels does not clot; it contains no solid fibrin, but this forms in it, sooner or later, when the blood gets by any means out of the vessels or when the lining of these is injured. In this way the mouths of the small vessels opened in a cut are clogged up, and the bleeding, which would otherwise go on indefinitely, is stopped.

So, too, when a surgeon ties up an artery before dividing it, the tight ligature crushes or tears its delicate inner surface, and the blood clots where that is injured, and from there a coagulum is formed reaching up to the next highest branch of the vessel. This becomes more and more solid, and by the time the ligature is removed has formed a firm plug in the cut end of the artery, which greatly diminishes the risk of bleeding.

The Source of Blood-fibrin. Since fresh blood-plasma contains no fibrin but does contain considerable quantities of other proteids, we look first to these as a possible source of the fibrin formed during coagulation. Blood drawn from a living animal into one third of its bulk of a cold saturated solution of magnesium sulphate and kept cold will not clot for a long time. The corpuscles slowly sink in the mixture, and after a time considerable quantities of colorless "salted" plasma can be drawn off from its upper part. The salted plasma still contains something which can form fibrin, for if diluted with six or seven times its volume of water it clots in a manner quite similar to pure blood-plasma (though the clot is a little less firm); and also, fibrin can be obtained by whipping it.

If salted plasma be saturated with sodium chloride it yields a whitish rather sticky precipitate, called *plasmine.* The remaining liquid is then found to have lost the power of clotting, but if the plasmine be treated with a little dilute saline solution it dissolves, and .the solution soon clots, with the formation of fibrin.

The plasmine is not a single body. If its solution before it clots have sodium chloride added to it in the proportion of about 15%, a white sticky precipitate is formed, and may be collected on a filter; it is a substance named *fibrinogen.* If more sodium chloride or some magnesium sulphate be added to the filtrate a second white precipitate is obtained: this is *paraglobulin.*

Paraglobulin dissolves in dilute solutions of common salt: such solutions cannot be made to yield fibrin, though they are coagulated with the formation of coagulated proteid (p. 10) at the temperature 75° C. (167° F). Purified fibrinogen also dissolves in dilute solution of common salt, and such solution is coagulated by heat (56° C. or 133° F.): but under certain conditions it clots with the formation of true fibrin. During the clotting the fibrinogen disappears, but

the quantity of fibrin formed never is quite equal in weight to the fibrinogen which disappears, so the process is not a mere direct transformation of one substance into the other.

We are thus led to the conclusion that the natural clotting of fresh blood is due to the formation of fibrin from fibrinogen which existed in solution in the plasma of the circulating blood and has been altered in the clotted, giving origin to fibrin. But as normal blood circulating in healthy uninjured blood-vessels does not clot nor do pure solutions of fibrinogen, we have still to seek the exciting cause of the change.

If to a solution of fibrinogen there be added a few drops of blood or of blood-serum, or of the washings of a blood-clot, fibrin will be formed; therefore drawn blood and serum and natural clot each contain something which can effect the conversion of fibrinogen into fibrin. This substance is the enzyme named *fibrin-ferment.*

The Fibrin-ferment. When blood-serum is treated with several times its volume of strong alcohol its various proteids and most of its salts are precipitated: if the precipitate be left standing in alcohol for some months the proteids become almost entirely insoluble in water, but a few drops of the watery extract cause clotting in a saline solution of fibrinogen, and clearly contain some of the ferment. A very minute quantity of the ferment will cause the conversion of an indefinite quantity of fibrinogen and does not appear to be itself used up in the process: it acts somehow by its mere presence, and the clotting of blood is to be relegated to that obscure group of physico-chemical processes known as catalytic. Solutions containing the ferment always give some proteid reactions and it may be a proteid, but this is doubtful; for the proteid present may be only an impurity. Watery solutions of ferment completely lose their activity when boiled.

If fibrinogen be dissolved in the least possible amount of dilute caustic potash and a few drops of as pure as possible a solution of fibrin ferment, freed from its salts by dialysis, be added, clotting does not occur: but it may be brought about by the addition of a very small quantity of a calcium salt. The presence of some calcium seems to be an essential, but the part it plays is unknown. Of the four substances which take part in the coagulation of blood, the fibrinogen

primarily determines the quantity of fibrin formed: the more fibrinogen the more fibrin, though never quite so much as the fibrinogen which disappears. The ferment acting on fibrinogen in the presence of a salt of calcium, in some way causes it to become fibrin, but does not itself enter into the fibrin; it is not used up in the process, and the amount of fibrin ultimately formed is the same whether much or little ferment be present; but the more ferment the quicker the clotting. The presence in small quantity of many neutral salts seems to favor coagulation, but none except the lime-salts are essential. The part they play is obscure; and when present in large proportions they prevent coagulation of blood or plasma, probably by hindering the formation of ferment. If fresh blood be mixed with an equal bulk of a saturated solution of magnesium sulphate (Epsom salts) or of common salt, it will not clot; but if this mixture be largely diluted with water, then some ferment is formed and clotting takes place.

The Proximate Causes of Normal Blood Coagulation. As all the phenomena of clotting, with the formation of fibrin agreeing in all respects with that formed during the natural coagulation of drawn blood, can be obtained in artificial solutions of fibrinogen, it is obvious that the process is not, as was once supposed, a so-called vital but a purely chemical one: but we still are far from a satisfactory explanation why the fibrinogen of the plasma does not clot in normal circulating blood contained in healthy blood-vessels. It is, in fact, much easier to point out what are not the proximate causes of the coagulation of drawn blood than what are.

Blood when removed from the Body and received in a vessel comes to rest, cools, and is exposed to the air, from which it may receive or to which it may give off gaseous bodies. But it is easy to prove that none of these three things is the cause of coagulation. Stirring the drawn blood and so keeping it in movement does not prevent but hastens its coagulation: and blood carefully imprisoned in a living blood-vessel, and so kept at rest, will not clot for a long time; not until the inner coat of the vessel begins to change from the want of fresh blood. Secondly, keeping the blood at the temperature of the Body hastens coagulation, and cooling retards it; blood received into an ice-cold vessel and kept surrounded with ice will clot more slowly than blood drawn and left exposed to ordinary temperatures. Finally, if the blood

be collected over mercury from a blood-vessel, without having been exposed to the air even for an instant, it will clot perfectly.

The formation of fibrin is then due to changes taking place in the blood itself when it is removed from the blood-vessels; the clotting depends solely upon some rearrangement of the blood-constituents, and the primary change seems to be the formation of fibrin-ferment. That healthy circulating blood contains no ferment but that this forms in drawn blood may be shown as follows: Blood is drawn from an artery into four separate vessels. To one specimen a large quantity of alcohol is added at once; to a second after five minutes, to a third after ten, to the fourth after fifteen. The precipitate in each is collected and dried, and then treated with water which will dissolve any ferment present. The watery extract from the first specimen will not cause clotting when added to a fibrinogen solution: from the second only slowly; the third more quickly, and the fourth quickest of all. It is hence concluded that there is no ferment in perfectly fresh blood, but that this begins to form as soon as blood is drawn and for some time goes on increasing, so that there is more in blood drawn ten minutes than in blood drawn only five. The alcohol in each sample precipitates all the ferment already present and prevents the formation of more. There is some evidence that a good many pale corpuscles disintegrate when blood is drawn, and it has been maintained that they then give origin to the fibrin-ferment along with other things: but of late evidence seems rather to point to the platelets as the main source of the ferment. As already stated they rapidly break down when blood is removed from the body, part of their substance going into solution in the plasma and part remaining as a sticky mass which tends to adhere to its fellows to form little clumps. If the formation of fibrin in clotting blood be watched with the aid of a microscope the fibrin threads are seen to appear first in the neighborhood of these clumps, and in many cases to radiate from them. Moreover those substances which check or retard the clotting of blood also hinder the disintegration of the platelets: and if a fine thread be passed through the blood-vessel of a living animal fibrin forms around it after a time, and this formation is preceded by adhesion to the thread and disintegration of platelets. But be the source of the ferment platelets or pale

corpuscles or both, we have still the problem why, under normal conditions, do not these break down in the circulating blood: have perchance the blood-vessels some part in the matter ?

Relation of the Blood-vessels to Coagulation. As to the rôle of the blood-vessels with respect to coagulation, two views are held, between which the facts at present known do not permit a decisive judgment to be made; and there may be some truth in both. One theory is that the vessels actively prevent coagulation by constantly absorbing from the blood some substance, as the fibrin-ferment, the presence of which is a necessary condition for the formation of fibrin and which is supposed to be constantly forming in the blood, but to be as steadily removed from it or destroyed by the lining cells of the blood-vessels. In support of this opinion is brought forward the fact that it is possible to inject considerable quantities of a solution of fibrin-ferment into the blood of a living animal without causing intravascular coagulation.

The other view is that the blood-vessels are passive. They simply do not excite those changes in the blood constituents which give rise to the formation of fibrin-ferment, while foreign bodies in contact with the blood do excite these changes and so lead to coagulation. In support of this view are brought forward the facts that drawn blood clots faster in vessels of such shapes that a large surface of blood is exposed to foreign contact; and that coagulation takes place rapidly in a vessel with a rough interior, while in a chemically clean glass vessel it occurs slowly. The experiment already mentioned of getting a clot around a thread passed through a blood-vessel, and also that of getting extensive clotting within the blood-vessels by the injection into a vein of extract of the thymus body, may be cited as tending to show that the linings of the blood-vessels cannot actively prevent coagulation; but it may be objected that in the one case locally, and in the other generally, the ferment is set free in the blood so fast that the vessels cannot remove it in time to prevent the formation of fibrin. Blood poured out from a torn vessel among other tissues of the body often clots very slowly; this may be due either to the tissues in general possessing the power of destroying fibrin-ferment or to their being merely indifferent substances not exciting the changes which lead to fibrin formation.

Whatever the part played by the blood-vessels in reference to coagulation it is only exhibited when their inner surfaces are healthy and uninjured. If their lining be ruptured or diseased the blood clots. Accordingly, after death, when post-mortem changes have affected the blood-vessels, the blood clots in them; but often very slowly, since the vessels only gradually alter. If the Body be left in one position after death the clots formed in the heart have often a marked buffy coat, because the corpuscles have had a long time to sink in the plasma before coagulation occurred. In medico-legal cases it is thus sometimes possible to say what was the position of a corpse for some hours after death, although it has been subsequently moved.

Lymph clots like the blood, but not so firmly. The clot formed is colorless.

Composition of the Blood. The average specific gravity of human blood is 1055. It has an alkaline reaction, which becomes less marked as coagulation occurs. About one half of its mass consists of moist corpuscles and the remainder of plasma. Exposed in a vacuum, 100 volumes of blood yield about 60 of gas consisting of a mixture of oxygen, carbon dioxide and nitrogen.

Chemistry of Serum. Blood-serum is plasma which has lost its fibrinogen and gained fibrin-ferment and probably some additional paraglobulin; from an analysis of it we can draw conclusions as to the plasma. In 100 parts of serum there are about 90 parts of water, 8.5 of proteids, and 1.5 of fats, salts and other less-known solid bodies. Of the proteids present the most abundant are serum-albumin and para-globulin. Serum-albumin agrees with egg-albumin in coagulating when heated: for this reason serum when boiled sets into an opaque white mass, just as the white of an egg does. Serum-albumin differs from egg-albumin in not being coagulated by ether; and in the fact that although present in such large quantities in the blood, it is not excreted by the kidneys, as egg-albumin is, if injected into a blood-vessel. The paraglobulin is also precipitated by heat, but may be precipitated alone by saturation of the serum with magnesium sulphate. Fats are present in the serum in small quantity except after a meal at which fatty substances have been eaten; serum obtained from the blood of an animal soon after such a meal is often milky in appearance from the large

amount of fats present, instead of being colorless or pale yellow and transparent as it is after fasting. The salts dissolved in the serum are mainly sodium chloride and carbonate; small quantities of sodium, calcium, and magnesium phosphates are also present.

Chemistry of the Red Corpuscles. In these in the fresh moist state there are, in 100 parts, 56 of water and 44 of solids. Of the solids about one per cent is salts, chiefly potassium phosphate and chloride. The remaining solids contain, in 100 parts, 90 of hæmoglobin and about 8 of other proteids; the residue consists of less well-known bodies.

Chemistry of the White Corpuscles. Besides much water, these yield several proteids, some fats, glycogen (see Chap. XXIX) and salts; and smaller quantities of other bodies. The predominant salts, like those of the red corpuscles, are potassium phosphates.

Variations in the Composition of the Blood. The above statements refer only to the average composition of the healthy blood and to its better known constituents. From what was said in the last chapter it is clear that the blood flowing from any organ will have lost or gained, or gained some things and lost others, when compared with the blood which entered it. But the losses and gains in particular parts of the Body are in such small amount as, with the exception of the blood-gases, to elude analysis for the most part: and the blood from all parts being mixed in the heart, they balance one another and produce a tolerably constant average. In health, however, the specific gravity of the blood may vary from 1045 to 1075; the red corpuscles also are present in greater proportion to the plasma after a meal than before it. Healthy sleep in proper amount leads to increase in the proportion of red corpuscles, and want of it tends to diminution of their number, as may be recognized in the pallid aspect of a person who has lost several nights' rest.

The proportion of the red corpuscles has a great importance since, as we shall subsequently see, they serve to carry oxygen, which is necessary for the performance of its functions, all over the Body. *Anæmia* is a diseased condition characterized by pallor due to deficiency of red blood-corpuscles, and accompanied by languor and listlessness. It is not unfrequent in girls on the verge of womanhood, and in per

sons overworked and confined within doors. In such cases the best remedies are open-air exercise and good food.

Summary. Practically the composition of the blood may be thus stated: It consists of (1) *plasma*, consisting of watery solutions of serum-albumin, paraglobulin, fibrinogen, sodium and other salts, and extractives of which the most constant are urea, kreatin, and grape-sugar; (2) *red corpuscles*, containing rather more than half their weight of water, the remainder being mainly hæmoglobin, other proteids, and potash salts; (3) *white corpuscles*, consisting of water, various proteids, glycogen, and potash salts; (4) the *platelets;* (5) *gases*, partly dissolved in the plasma or combined with its sodium salts, and partly combined (oxygen) with the hæmoglobin of the red corpuscles.

Quantity of Blood. The total amount of blood in the Body is difficult of accurate determination. It is about $\frac{1}{13}$ of the whole weight of the Body, so the quantity in a man weighing 75 kilos (165 lbs.) is about 5.8 kilos (12.7 lbs.). Of this at any given moment about one fourth would be found in the heart, lungs and larger blood-vessels; and equal quantities in the vessels of the liver, and in those of the muscles which move the skeleton; while the remaining fourth is distributed among the remaining parts of the Body.

The Origin and Fate of the Blood-corpuscles. The white blood-corpuscles vary so rapidly and frequently in number in the blood that they must be constantly in process of alteration or removal, and formation; their number is largely increased after taking food, even more than that of the red, so that their proportion to the red rises, from 1 to 1000 during fasting, to 1 to 250 or 300 after a meal. This increase is mainly due to increased flow of lymph at this time through the lymphatics of the alimentary canal which have much lymphoid tissue on their course; and, as already pointed out, lymph-corpuscles are constantly multiplying in this tissue and are gathered from it by the lymph, to be poured into the blood (see also Chap. XXIII). Migrated pale corpuscles of the blood and the leucocytes of the lymph retain many of the characters of undifferentiated and unspecialized embryonic cells; and there is some evidence that they may develop new tissues in the repair of injured parts.

Amphioxus, the lowest undoubted vertebrate animal (see Zoology), possesses only colorless corpuscles in its blood.

Higher and more complex animals need more oxygen and, as blood-plasma dissolves very little of that gas, they develop in addition the hæmoglobin-containing corpuscles which pick it up in the gills or lungs and carry it to all parts of the Body, leaving it where wanted (see Chap. XXVI). In cold-blooded vertebrates the red corpuscles are not nearly so many in proportion as in the warm-blooded, which use far more oxygen. The older view was that the mammalian red corpuscle represented the nucleus of one of the white, in which hæmoglobin had been formed and from about which the rest of the corpuscle had disappeared. This, however, does not seem to be the case. In adults new red blood-corpuscles are formed by the segregation of portions of the protoplasm of peculiar cells (*hæmatoblasts*) found in various parts of the Body, but especially in the *red marrow* of certain bones (p. 95). In the embryo some cells of the liver, and in new-born animals (possibly also in adult) some connective-tissue corpuscles (p. 112) form new red blood-corpuscles.

How long an individual red corpuscle lasts is not known, nor with certainty how or where it disappears : there is, however, some reason to believe that many are finally destroyed in the spleen (see Chap. XXIII). Their average rate of disappearance and new formation is unknown, but in emergencies (as after severe hæmorrhages) they can be reproduced with great rapidity.

Chemistry of Lymph. Lymph is a colorless fluid when pure, feebly alkaline, and with a specific gravity of about 1045. It may be described as blood minus its red corpuscles and much diluted, but of course in various parts of the Body it will contain minute quantities of substances derived from neighboring tissues. It contains a considerable quantity of carbon dioxide gas which it gives up in a vacuum, but no uncombined oxygen, since any of that gas which passes into it by diffusion from the blood is immediately picked up by the living tissues among which the lymph flows.

CHAPTER VI.

.THE SKELETON.

Exoskeleton and Endoskeleton. The skeleton of an animal includes all its hard protecting or supporting parts, and is met with in two main forms. One is an *exoskeleton* developed in connection with either the superficial or deeper layer of the skin, and represented by the shell of a clam, the scales of fishes, the horny plates of a turtle, the bony plates of an armadillo, and the feathers of birds. In man the exoskeleton is but slightly developed, but it is represented by the hairs, nails and teeth; for although the latter lie within the mouth, the study of development shows that they are developed from an offshoot of the skin which grows in and lines the mouth long before birth. Hard parts formed from structures deeper than the skin constitute the *endoskeleton*, which in man is highly developed and consists of a great many *bones* and *ca,tilages* or gristles, the bones forming the mass of the hard framework of the Body, while the cartilages finish it off at various parts. This framework is what is commonly meant by the skeleton; it primarily supports all the softer parts and is also arranged so as to surround cavities in which delicate organs, as the brain, heart or spinal cord, may lie with safety. The gross skeleton thus formed is completed and supplemented by another made of the *connective tissues*, which not only, in the shape of tough bands or *ligaments*, tie the bones and cartilages together, but also in various forms pervade the whole Body as a sort of subsidiary skeleton running through all the soft organs and forming networks of fibres around their other constituents; they make, as it were, a microscopic skeleton for the individual modified cells of which the Body is so largely composed, and also form partitions between the muscles, cases for such organs as the liver and kidneys, and sheaths around the blood vessels. The bony and cartilaginous framework with its ligaments might be called the skele-

ton of the organs of the Body, and this finer supporting meshwork the skeleton of the tissues. Besides forming a support in the substance of various organs, the connective tissues are often laid down as a sort of packing material in the crevices between them; and so widely are they distributed everywhere from the skin outside to the lining of the alimentary canal inside, that if some solvent could be employed which would corrode away all the rest and leave only these tissues, a very perfect model of the whole Body would be left; something like a "skeleton leaf," but far more minute in its . tracery.

The Bony Skeleton (Fig. 16). If the hard framework of the Body were joined together like the joists and beams of a house, the whole mass would be rigid; its parts could not move with relation to one another, and we should be unable to raise a hand to the mouth or put one foot before another. To allow of mobility the bony skeleton is made of many separate pieces which are joined together, the points of union being called *articulations*, and at many places the bones entering into an articulation are movably hinged together, forming what are known as *joints*. The total number of bones in the Body is more than two hundred in the adult; and the number in children is still greater, for various bones which are distinct in the child (and remain distinct throughout life in many lower animals) grow together so as to form one bone in the full-grown man. The adult bony skeleton may be described as consisting of an *axial skeleton*, found in the head, neck and trunk; and an *appendicular skeleton*, consisting of the bones in the limbs and in the arches (*u* and *s*, Fig. 16) by which these are carried and attached to the trunk.

Axial Skeleton. The axial skeleton consists primarily of the *vertebral column* or *spine*, a side view of which is represented in Fig. 17. The upper part of this column is composed of twenty-four separate bones, each of which is a *vertebra*. At the posterior part of the trunk, beneath the movable vertebræ, comes the sacrum (*S* 1), made up of five vertebræ, which in the adult grow together to form one bone, and below the sacrum is the *coccyx* (*Co* 1-4), consisting of four very small tail vertebræ, which in advanced life also unite to form one bone.

On the top of the vertebral column is borne the *skull*, made up of two parts, viz., a great box above which incloses

the brain and is called the *cranium*, and a large number of

FIG. 16.—The bony and cartilaginous
skeleton.

FIG. 17.—Side view of the
spinal column.

bones on the ventral side of this which form the skeleton of

the face. Attached by ligaments to the under side of the cranium is the *hyoid bone,* to which the root of the tongue is fixed.

Of the twenty-four separate vertebræ of the adult the seven nearest the skull (Fig. 17, *C* 1-7) lie in the neck and are known as the *cervical vertebræ.* These are followed by twelve others which have *ribs* attached to them (see Fig. 16) and lie at the back of the chest; they are the *thoracic* or *dorsal vertebræ* (*D* 1-12). The ribs (Fig. 28) are slender curved bones attached by their dorsal ends, called their *heads,* to the thoracic vertebræ and running thence round the sides of the chest. In the ventral median line of the latter is the breast-bone or *sternum* (*d,* Fig. 16). Each rib near its sternal end ceases to be bony and is composed of cartilage.

These parts—skull, hyoid bone, vertebral column, ribs, and sternum—constitute the axial skeleton.

The Thoracic or Dorsal Vertebræ. If a single vertebra, say the eleventh from the skull, be examined carefully it will be found to consist of the following parts (Figs. 18 and 19):

First a bony mass, *C,* rounded on the sides and flattened on each end where it is turned towards the vertebræ above and below it. This stout bony cylinder is the "*body*" or *centrum* of the vertebra, and the series of vertebral bodies (Fig. 17) forms in the trunk that bony partition between the dorsal and ventral cavities of the body spoken of in Chapter I. To the dorsal side of the body is attached an arch—the *neural arch, A,* which with the back of the *body* incloses a space, *Fv,* the *neural ring.* In the tube formed by the rings of the successive vertebræ lies the spinal cord. Projecting from the dorsal side of the neural arch is a long bony bar, *Ps,* the *spinous process :* and the projections of these processes from the various vertebræ can be felt through the skin all down the middle of the back. Hence the name of *spinal column* often given to the whole back-bone.

Six other processes arise from the arch of the vertebra: two project forwards, *i.e.,* towards the head; these, *Pas,* are the *anterior articular processes* and have smooth surfaces, covered with cartilage, on their dorsal sides. A pair of similar *posterior articular processes, Pai,* runs back from the neural arch, and these have smooth surfaces on their ventral aspects. In the natural position of the vertebra, the smooth surfaces of its anterior articular processes fit upon the poste-

rior articular processes of the vertebra next in front, forming a joint, and the two processes are united by ligaments. Sim-
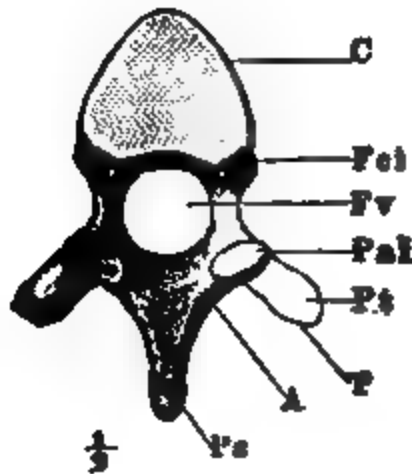
Fig. 18.   Fig. 19.

Fig. 18.—A thoracic vertebra seen from behind, *i.e.*, the end turned from the head. Fig. 19 —Two thoracic vertebræ viewed from the left side, and in their natural relative positions. *C*, the body ; *A*, neural arch ; *Fr*, the neural ring ; *Ps*, spinous process; *Pns*, anterior articular process ; *Pas*, posterior articular process ; *Pt*, transverse process ; *Ft*, facet for articulation with the tubercle of a rib ; *Fcs*, *Fci*, articular surfaces on the centrum for articulation with a rib.

ilarly its posterior articular processes form joints (Fig. 19) with the anterior articular processes of the vertebra next behind.

The remaining processes are the *transverse, Pt,* which run outwards and a little dorsally. Each of these has a smooth articular surface, *Ft,* near its outer end.

On the " body " are seen two articular surfaces on each side: one, *Fcs,* at its anterior, the other, *Fci,* at its posterior end, and both close to the attachment of the neural arch. Each of these surfaces forms with corresponding areas on the vertebræ in front and behind a pit into which the end of a rib fits and the rib attached in this way to the anterior part of the " body " is also fitted on, a little way from its dorsal end, to the articular surface at the end of the transverse process.

The Segments of the Axial Skeleton. If a thoracic vertebra, say the first (Fig. 20), be detached with the pair of ribs, *Cv,* belonging to it and the bit of the sternum, *S,* to which these ribs are fixed ventrally, we would find a bony partition formed by the body of the vertebra, lying between

two arches which surround cavities. The dorsal cavity inclosed by the "body" and "neural arch" contained originally part of the spinal cord. The other ring, made up by the body of the vertebra dorsally, the sternum ventrally, and the ribs on the sides, surrounds the chest-cavity with its contents. All of these parts together form a typical segment of the axial skeleton, which, however, only attains this completeness in the thoracic region of the trunk. In the skull it is greatly modified; and in the neck and the lower part of the trunk the ribs are either absent or very small, appearing only as processes of the vertebræ; and the sternal portion is wanting altogether.

Fig. 20.—Diagrammatic representation of a segment of the axial skeleton. *V*, a vertebra; *C, Cv*, ribs articulating above with the body and transverse process of the vertebra; *S*, the breast-bone. The lighter-shaded part between *S* and *C* is the rib-cartilage.

Nevertheless we may regard the whole axial skeleton as made up of a series of such segments placed one in front of another, but having different portions of the complete segment much modified or rudimentary or even altogether wanting in some regions. Parts which in this way really correspond to one another though they differ in detail, which are so to speak different varieties of one thing, are said in anatomical language to be *homologous* to one another; and when they succeed one another in a row, as the trunk segments do, the *homology* is spoken of as *serial*.

The Cervical Vertebræ. In the cervical region of the vertebral column the bodies of the vertebræ are smaller than in the dorsal, but the arches are larger; the spinous processes are short and often bifid and the transverse processes appear to be perforated by a canal, the *vertebral foramen.* The bony bar bounding this aperture on the ventral side, however, is in reality a very small rib which has grown into continuity with the body and true transverse process of
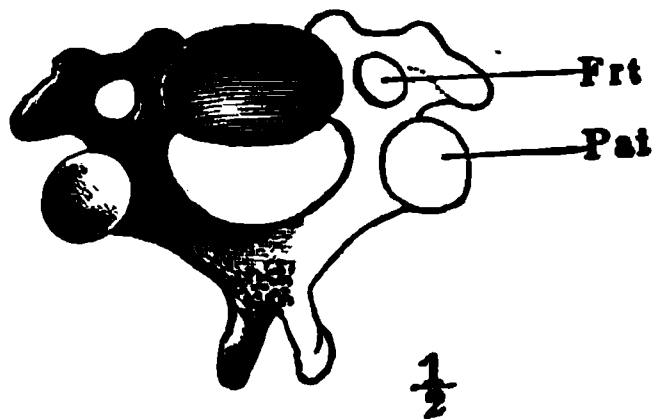
Fig. 21.—A cervical vertebra. *Frt*, vertebral foramen; *Pai*, anterior articular process.

the vertebra, although separate in very early life: the transverse process proper bounds the vertebral foramen dorsally. In this latter during life runs an artery, which ultimately enters the skull-cavity.

The Atlas and Axis. The first and second cervical vertebræ differ considerably from the rest. The first, or *atlas* (Fig. 22), which carries the head, has a very small body, *Aa*, and a large neural ring. This ring is subdivided by a cord, the *transverse ligament*, *L*, into a dorsal moiety in which the spinal cord lies and a ventral into which the bony process D projects. This is the *odontoid process*, and arises from the front of the axis or second cervical vertebra (Fig. 23). Around this peg the atlas rotates when the head is turned from side to side, carrying the skull (which articulates with the large hollow surfaces *Fas*) with it.

The odontoid process really represents a large piece of the body of the atlas which in early life separates from its own vertebra and becomes united to the axis.

The Lumbar Vertebræ (Fig. 24) are the largest of all the movable vertebræ and have no ribs attached to them. Their spines are short and stout and lie in a more horizontal plane
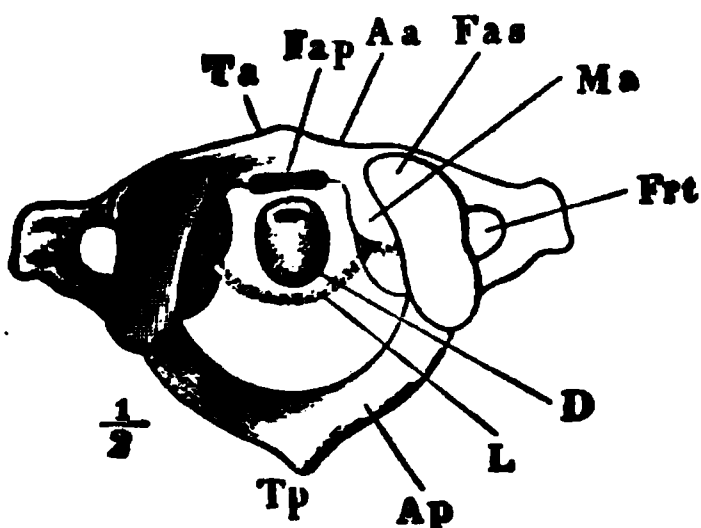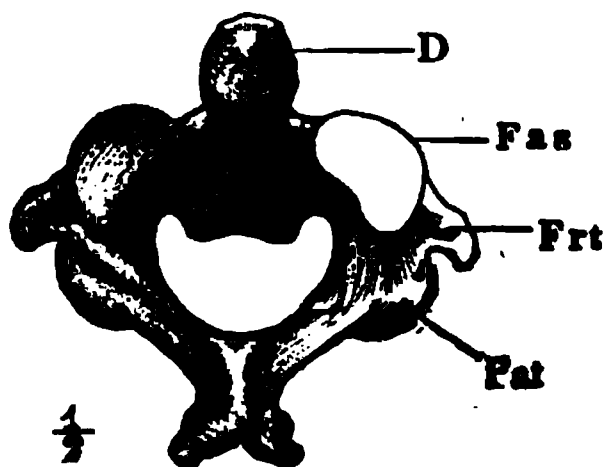
FIG. 22.   FIG. 23.

FIG. 22.—The *atlas*. FIG. 23.—The *axis*. *Aa*. body of atlas; *D*, odontoid process; *Fas*, facet on front of atlas with which the skull articulates; and in Fig. 23, anterior articular surface of axis; *L*, transverse ligament; *Frt*, vertebral foramen; *Ap*, neural arch; *Tp*, spinous process.

than those of the vertebræ in front. The articular and transverse processes are also short and stout.

The Sacrum, which is represented along with the last lumbar vertebra in Fig. 25, consists in the adult of a single bone; but cross-ridges on its ventral surface indicate the limits of the five separate vertebræ of which it is composed in childhood. It is somewhat triangular in form, its base

being directed upwards and articulating with the under surface of the body of the fifth lumbar vertebra. On its sides are large surfaces to which the arch bearing the lower

.

Fig. 14.—A lumbar vertebra seen from the left side. *Ps*, spinous process; *Pas*, anterior articular process; *Pai*, posterior articular process; *Pt*, transverse process.

Fig. 15.—The last lumbar vertebra and the sacrum seen from the ventral side. *Fso*, anterior sacral foramina.

limbs is attached (see Fig. 16). Its ventral surface is concave and smooth and presents four pairs of *anterior sacral*

foramina, Fsa, which communicate with the neural canal. Its dorsal surface, convex and roughened, has four similar pairs of *posterior sacral foramina.*

The *coccyx* (Fig. 26) calls for no special description. The four bones which grow together, or *ankylose,* to form it, represent only the bodies of vertebræ, and even those incompletely. It is in reality a short tail, although not visible as such from the exterior.
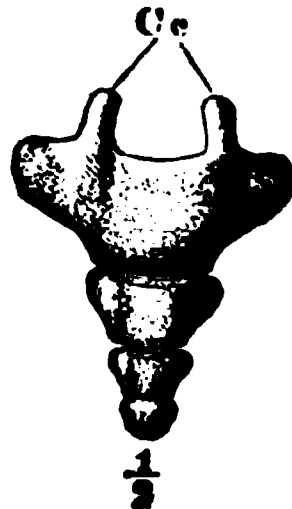
The Spinal Column as a Whole. The vertebral column is in a man of average height about twenty-eight inches long. Viewed from the side (Fig. 17) it presents four curvatures; one with the convexity forwards in the cervical

Fig. 26.
The coccyx.

region is followed, in the thoracic, by a curve with its concavity towards the chest. In the lumbar region the curve has again its convexity turned ventrally, while in the sacral and coccygeal regions the reverse is the case. These curvatures give the whole column a good deal of springiness such as would be absent were it a straight rod, and this is farther secured by the presence of compressible elastic pads, the *intervertebral disks,* made up of cartilage and connective tissue, which lie between the bodies of those vertebræ which are not ankylosed together, and fill up completely the empty spaces left between the bodies of the vertebræ in Fig. 17. By means of these pads, moreover, a certain amount of movement is allowed between each pair of vertebræ; and so the spinal column can be bent to considerable extent in any direction; while the movement between any two vertebræ is so limited that no sharp bend can take place at any one point, such as might tear or otherwise injure the spinal cord contained in the neural canal. The amount of movement permitted is greatest in the cervical region.

In the case of the movable vertebræ, the arch is somewhat narrowed where it joins the body on each side ; this narrowed stalk is the *pedicle* (*Ii,* Fig. 19), while the broader remaining portion of the arch is its *lamina.* Between the pedicles of two contiguous vertebræ there are in this way left apertures, the *intervertebral* holes which form a series on each side of the vertebral column, and one of which, *Fi,* is shown between the two dorsal vertebræ in Fig. 19. Through these foramina nerves run out from the spinal cord

to various regions of the Body. The sacral foramina, anterior and posterior, are the representatives of these apertures, but modified in arrangement, on account of the fusion of the arches and bodies of the vertebræ between which they lie.

Sternum. The *sternum* or *breast-bone* (Fig. 27 and *d*, Fig. 16) is wider from side to side than dorso-ventrally. It consists in the adult of three pieces, and seen from the ventral side has somewhat the form of a dagger. The piece *M* nearest the head is called the *handle* or *manubrium*, and presents anteriorly a notch, *Icl*, on each side, with which the collar-bone articulates (*u*, Fig. 16); farther back are two other notches, *Ic*1 and *Ic*2, to which the sternal ends of the first and second ribs are attached. The middle piece, *C*, of the sternum is called the *body;* it completes the notch for

the second rib and has on its sides others, *Ic* 3–7, for the third, fourth, fifth, sixth, and seventh ribs. The last piece of the sternum, *P*, is the *ensiform* or *xiphoid process;* it is composed of cartilage, and has no ribs attached to it.

The Ribs. (Fig. 28). There are twelve pairs of ribs, each being a slender curved bone attached dorsally to the body and transverse process of a vertebra in the manner already mentioned, and continued ventrally by a *costal cartilage.* In the case of the anterior seven pairs, the costal cartilages are attached directly to the sides of the breast-bone; the next three cartilages are each attached to the cartilage of the preceding rib, while the cartilages of the eleventh and twelfth ribs are quite unattached ventrally, so these are called the *free* or *floating ribs.* The convexity of each curved rib is turned outwards so as to give roundness to the sides of the

Fig. 27.—The sternum seen on its ventral aspect. *M*, manubrium; *C*, body; *P*, xiphoid process; *Icl*, notch for the collar-bone; *Ic* 1–7, notches for the rib-cartilages.

chest and increase its cavity, and each slopes downwards from its vertebral attachment, so that its sternal end is considerably lower than its dorsal.

The Skull. (Fig. 29) consists of twenty-two bones in the adult, of which eight, forming the *cranium*, are arranged so as to inclose the brain-case and protect the auditory organ,

while the remaining fourteen support the face and surround the mouth, the nose, and the eye-sockets.

FIG. 23.—The ribs of the left side, with the dorsal and two lumbar vertebræ, the rib-cartilages and the sternum; *a*, first and, *b*, twelfth thoracic vertebra; *c*, first lumbar vertebra.

Cranium. The cranium is a box with a thick floor and thinner walls and roof. Its floor or *base* represents in the head (as is depicted in the diagram Fig. 2) that partition between the dorsal and ventral cavities which in the trunk is made up of the bodies of the vertebræ. In very early life it

presents in the middle line a series of four bones, the *basi-occipital, basi-sphenoid, presphenoid,* and *basi-ethmoid,* which answer pretty much to the bodies of four vertebræ, and have attached to them the thin bones which inclose the skull-cavity (which may be likened to an enlarged neural canal) on the sides and top. In the Human Body, however, these bones

Top

Fig. 29 —A side view of the skull. O, occipital bone ; T, temporal ; Pr, parietal ; F, frontal, S, sphenoid ; Z, malar ; Mx, maxilla; N, nasal; E, ethmoid; L, lachrymal; Md, inferior maxilla.

very soon ankylose with others or with one another; although they remain distinct throughout life in the skulls of very many lower animals. On the base of the skull, besides many small apertures by which nerves and blood-vessels pass in or out, is a large aperture, the *foramen magnum,* through which the spinal cord passes in to join the brain.

The cranial bones are the following:

1. The *occipital bone* (Fig. 29, *O*), unpaired and having in it the *foramen magnum.* It is made up by the fusion of the basi-occipital with other flatter bones.

2. The *frontal bone* (Fig. 29, *F*), also unpaired in the adult, but in the child each half is a separate bone. 3. A pair of thin platelike *parietal bones* (Fig. 29, *Pr*) which meet one another along the middle line in the top of the skull, and roof-in a great part of the cranial cavity. 4. A pair of *temporal bones* (Fig. 29, *T*), one on each side of the skull below the parietal. On each temporal bone is a large aperture leading into the ear-cavity, the essential parts of the organs of hearing being contained in these bones. 5. The *sphenoid bone*, made up by the union of the *basi-sphenoid* and *pre-sphenoid* (lying on the base of skull in front of the basi-occipital) with one another and with flatter bones, is seen partly (Fig. 29, *S*) on the sides of the cranium in front of the temporals. 6.

Fig. 30.—The base of the skull. The lower jaw has been removed. At the lower part of the figure is the hard palate forming the roof of the mouth and surrounded by the upper set of teeth. Above this are the paired openings of the posterior nares, and a short way above the middle of the figure is the large median *foramen magnum*, with the bony convexities (or *occipital condyles*) which articulate with the atlas, on its sides.

The *ethmoid*, like the sphenoid, single in the adult, is really made up by the union of a single median *basi-ethmoid* with a pair of lateral bones. It closes the skull-cavity in front, and lies between it and the top of the nasal chambers, being perforated by many small holes through which the nerves of smell pass. A little bit of it is seen on the inner side of the eye socket at *E* in Fig. 29.

Facial Skeleton. The majority of the face-bones are in pairs; two only being single and median. One of these is the lower jaw-bone or *inferior maxilla* (Fig. 29, *Md*); the other is the *vomer*, which forms part of the partition between the two nostrils.

The paired face-bones are: 1. The *maxillæ*, or upper jaw-bones (*Mx*, Fig. 29), one on each side, carrying the upper row of teeth and forming a great part of the *hard palate*, which separates the mouth from the nose. 2. The *palatine bones*, completing the skeleton of the hard palate, and behind

which the nose communicates by the *posterior nares* (Fig. 30) with the throat-cavity, so that air can pass in or out in breathing. 3. The *malar bones*, or cheek-bones, (*Z*, Fig. 29.) lying beneath and on the outside of the orbit on each side. 4. The *nasal bones* (*N*, Fig. 29), roofing in the nose. 5. The *lachrymal bones* (*L*, Fig. 29), very small and thin and lying between the nose and orbit. 6. The *inferior turbinate bones*, lying inside the nose, one in each nostril-chamber.

The Hyoid. Besides the cranial and facial bones there is, as already pointed out, one other, the *hyoid* (Fig. 31), which really belongs to the skull, although it lies in the neck. It can be felt in the front of the throat, just above "Adam's apple." The hyoid bone is U-shaped, with its con-

vexity turned ventrally, and consists of a *body* and two pairs of processes called *cornua*. The smaller cornua (Fig. 31, 3) are attached to the base of the skull by long ligaments. These ligaments in many animals are represented by bones, so that the hyoid, with them, forms a bony arch attached to the base of the skull much as the ribs are attached to the bodies of the vertebræ. In fishes behind this *hyoidean arch* come several others which bear the gills; and in the very young Human Body these also are represented, though they almost entirely disappear long before birth. The hyoid, then, with its cornua and ligaments answers pretty much to a gill-arch, or really to parts of two gill-arches, since the great and small cornua belong to originally separate arches present at an early stage of development. It is a remnant of a structure which has no longer any use in the Human Body; but in the young frog-tadpole parts answering to it carry gills and have clefts between them which extend into the throat just as in fishes. The gills are lost afterwards and the clefts closed up when the frog gets its lungs and begins to breathe by them. In the embryonic human being these gill-clefts are also present and several more behind them, but the arches between them do not bear gills, and the clefts themselves are closed long before birth. As they have no use their presence is hard to account for; those who accept the doctrine of evolution regard them as developmental reminiscences of an extremely remote ancestor in which they were of functional importance somewhat as in the tadpole: of

Fig. 31.—The hyoid bone. 1, body; 2, great cornua; 3, small cornua.

course this does not mean that men were developed from tadpoles.

The Appendicular Skeleton. This consists of the *shoulder-girdle* and the bones of the fore limbs, and the *pelvic girdle* and the bones of the posterior limbs. The two supporting girdles in their natural position with reference to the trunk skeleton are represented in Fig. 32.

The Shoulder-girdle, or Pectoral Arch. This is made up, on each side, of the *scapula* or *shoulder-blade,* and the *clavicle* or collar-bone.

The *scapula* (*S,* Fig. 32) is a flattish triangular bone which can readily be felt on the back of the thorax. It is not directly articulated to the axial skeleton, but lies imbedded in the muscles and other parts outside the ribs on each side of the vertebral column. From its dorsal side arises a crest to which the outer end of the collar-bone is fixed, and on its outer edge is a shallow cup into which the top of the arm-bone fits: this hollow is known as the *glenoid fossa.*

The *collar-bone* (*C,* Fig. 32) is cylindrical and attached at its inner end to the sternum as shown in the figure, fitting into the notch represented at *Icl* in Fig. 27.

The Fore Limb. In the limb itself (Fig. 33) are thirty bones. The largest, *a,* lies in the upper arm, and is called the *humerus.* At the elbow the humerus is succeeded by two bones, the *radius* and *ulna, c* and *b,* which lie side by side, the radius being on the thumb side. At the distal ends of these bones come eight small ones, closely packed and forming the wrist, or *carpus.* Then como five cylindrical bones which can be felt through the soft parts in the palm of the hand; one for the thumb, and one for each of the fingers. These are the *metacarpal bones,* and are distinguished as first, second, third, and so on, the first being that of the thumb. In the thumb itself are two bones, and in each finger three, arranged in rows one after the other; these bones are all called *phalanges.*

The Pelvic Girdle (Fig. 32). This consists of a large bone, the *os innominatum, Oc,* on each side, which is firmly fixed dorsally to the sacrum and meets its fellow in the middle ventral line. In the child each os innominatum consists of three bones, viz., the ilium, the ischium, and pubis. Where these three bones meet and finally ankylose there is a deep socket, the *acetabulum,* into which the head of the thigh-

bone fits (see Fig. 16). Between the pubic and ischial bones is the largest foramen in the whole skeleton, known as the doorlike or *thyroid foramen*. The pubic bone lies above

Fig. 34.—The skeleton of the trunk and the limb arches seen from the front. *C*, clavicle; *S*, scapula, *Oc*, innominate bone attached to the side of the sacrum dorsally and meeting its fellow at the *pubic symphysis* in the ventral median line.

and the ischial below it. The ilium forms the upper expanded portion of the os innominatum to which the line drawn from *Oc* in Fig. 32 points.

The Hind Limb. In this there are thirty bones, as in the fore limb, but not quite similarly arranged; there being one less at the ankle than in the wrist, and one at the knee not present at the elbow-joint. The thigh-bone or *femur* (*a*, Fig. 34) is the largest bone in the body and extends from the hip to the knee-joint. It presents above a large rounded *head* which fits into the acetabulum and, below, it is also

enlarged and presents smooth surfaces which meet the bones of the leg. These latter are two in number, known as the *tibia, c,* or shin-bone, and *fibula, d;* the tibia being on the great-toe side. In front of the knee-joint is the knee-cap, or *patella, b.*

Fig. 33.   Fig. 34.

Fig. 33.—The bones of the arm. *a,* humerus; *b,* ulna; *c,* radius; *d,* the carpus; *e,* the fifth metacarpal; *f,* the three phalanges of the fifth digit (little finger); *g,* the phalanges of the pollex (thumb).

Fig. 34. - Bones of the leg *a,* femur; *b,* patella; *c,* tibia; *d,* fibula; *h,* calcaneum; *e,* remaining tarsal bones; *f,* metatarsal bones; *g,* phalanges.

At the distal end of the leg-bones comes the *foot,* consisting of *tarsus, metatarsus,* and *phalanges.* The tarsus, which answers to the carpus of the fore limb, is made up of seven irregular bones, the largest being the heel-bone, or *calcaneum,*

h. The metatarsus consists of five bones lying side by side, and each carries a toe at its distal end. In the great toe (or *halluz*) there are two phalanges, in each of the others three, arranged as in the fingers, but smaller.

Comparison of the Anterior and Posterior Limbs. It is clear that the skeletons of the arm and leg correspond pretty
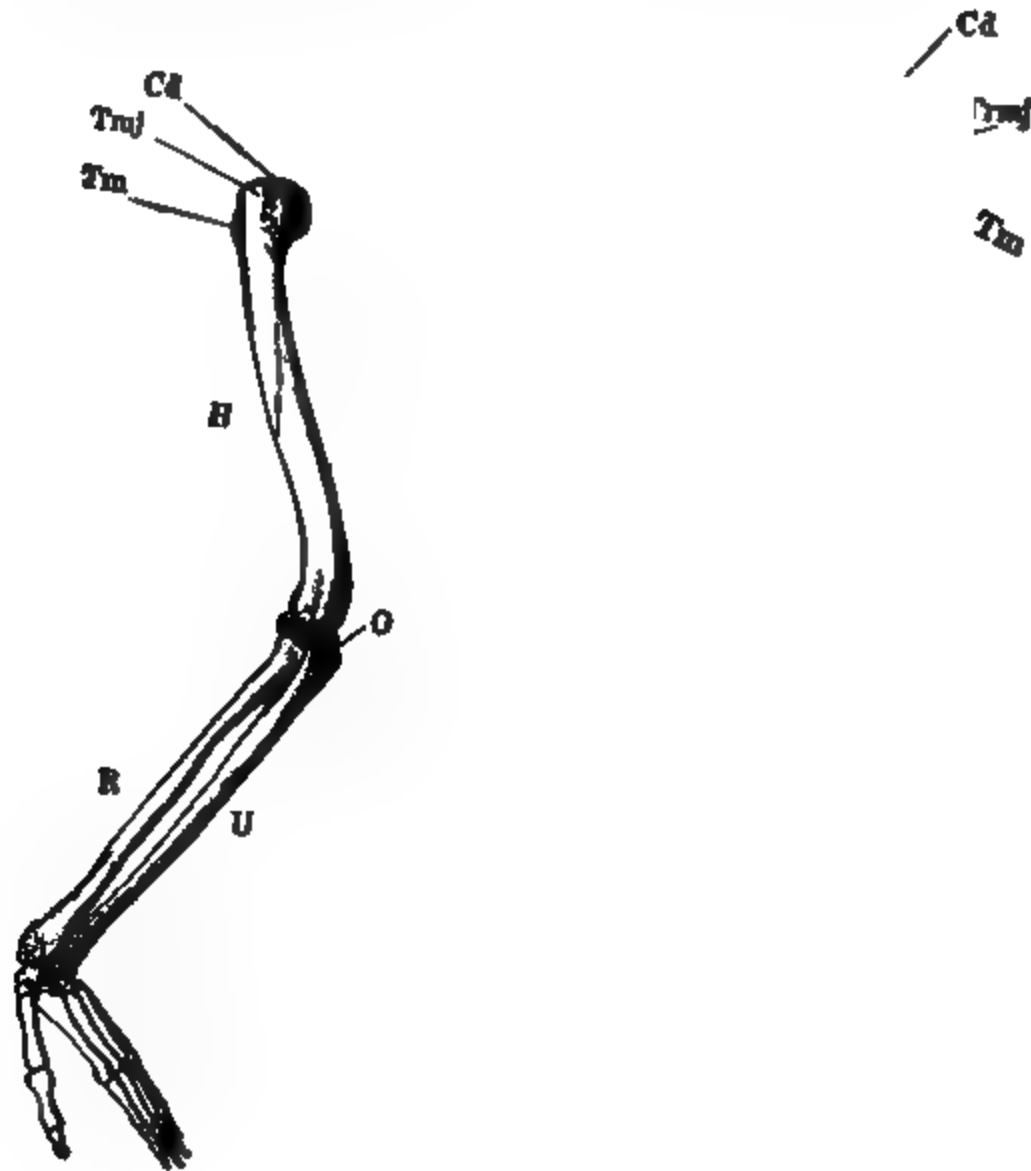
35.—The skeleton of the arm and leg. *H,* the humerus; *Cd,* its articular 'hich fits into the glenoid fossa of the scapula; *U,* the ulna; *R,* the radius; olecranon; *Fe,* the femur; *P,* the patella; *Ft,* the fibula; *T,* the tibia.

ly to one another. They are in fact quite alike in very
life, and their differences at birth depend upon their
.g different ways as they develop from their primitive

simplicity; as both may be regarded as modifications of the same original structure, they are *homologous*. The pelvic girdle clearly corresponds generally to the pectoral arch, the tibia and fibula to the radius and ulna; the five metatarsal bones to the five metacarpal, and the phalanges of the toes to those of the thumb and fingers. On the other hand, there is in the arm no separate bone at the elbow-joint corresponding to the patella at the knee, but the ulna bears above a bony process, the *olecranon* (*O*, Fig. 35), which at first is a separate bone and is the representative of the patella. There are in the carpus eight bones and in the tarsus but seven. The
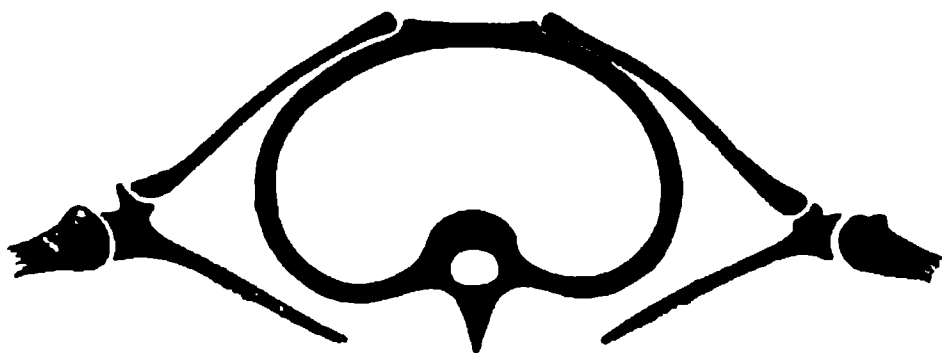
Fig. 36.—Diagram showing the relation of the pectoral arch to the axial skeleton.

astragalus of the tarsus (*Ta*, Fig. 38) represents, however, *two* bones which have grown together. The elbow-joint bends ventrally and the knee-joint dorsally.

Comparing the limbs as a whole, greater differences come to light, differences which are mainly correlated with the different uses of the two limbs. The arms, serving as prehensile organs, have all their parts as movable as is consistent with the requisite strength, while the lower limbs, having to bear the whole weight of the Body,
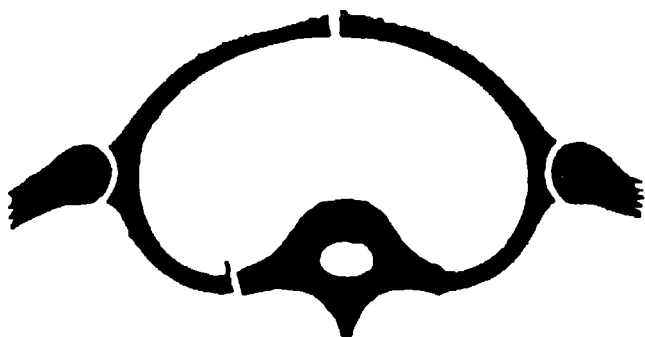
Fig. 37.—Diagram showing the attachment of the pelvic arch to the axial skeleton.

require to have their parts much more firmly knit together. Accordingly we find the shoulder-girdle, represented red in the diagram (Fig. 36), only directly attached to the axial skeleton by the union of the inner ends of the clavicles with the sternum, and capable of considerable independent movement, as seen, for instance, in "shrugging the shoulders."

The pelvic arch, on the contrary, is firmly and immovably fixed to the sides of the sacrum. The socket of the scapula, into which the head of the humerus fits, is very shallow and allows a far greater range of movement than is permitted by the deeper socket on the pelvis, into which the head of the femur fits. Further, if we hold the right humerus tightly in the left hand and do not allow it to move, we can still move the forearm bones so as to turn the palm of the hand either up or down: no such movement is possible between the tibia and fibula. Finally, in the foot the bones are much less movable than in the hand, and are arranged so as to make a springy arch (Fig. 38) which bears behind on the calcaneum, *Ca*, and in front on the distal ends of the metatarsal bones, *Os*; over the crown of the arch, at *Ta*, is the surface with

Ta

la

᠊᠊ᴐ   Tᴅ   ᴗᵒ   Sᴀ̍ʙ̍   s

Fɪɢ. 38.—The bones of the foot. *Ca*, *calcaneum*, or *os calcis* ; *Th*, articular sur-face for tibia on the *astragalus* ; *N*, scaphoid bone ; *CI*, *CII*, first and second cuneiform bones'; *Cb*, cuboid bone ; *MI*, metatarsal bone of great toe.

which the leg-bones articulate and on which the weight of the Body bears in standing.

The toes, too, are far less movable than the fingers, and this difference is especially well marked between the great toe and the thumb. The latter can be made to meet each of the finger-tips and so the hand can seize and manipulate very small objects, while this power of *opposing* the first digit to the rest is nearly absent in the foot of civilized man. In children, however, who have never worn boots, and in savages, the great toe is far more movable, though it never forms as complete a thumb as in many apes, which use their feet, as well as their hands, for prehension. By practice, however, our own toes can be made much more mobile than they usually are, so that the foot can to a certain extent replace the hand; as has been illustrated in the case of persons born

without hands who have learned to write and paint with their toes.

Peculiarities of the Human Skeleton. These are largely connected with the division of labor between the fore and hind limbs referred to above, which is carried farther in man than in any other creature. Even the highest apes frequently use their fore limbs in locomotion and their hind limbs in prehension, and we find accordingly that anatomically they present less differentiation of hand and foot. The other more important characteristics of the human skeleton are correlated for the most part with the maintenance of the erect posture, which is more complete and habitual in man than in the animals most closely allied to him anatomically. These peculiarities, however, only appear fully in the adult. In the infant the head is proportionately larger, which gives the centre of gravity of the Body a comparatively very high position and renders the maintenance of the erect posture difficult and insecure. The curves of the vertebral column are nearly absent, and the posterior limbs are relatively very short. In all these points the infant approaches more closely than the adult to the ape. The subsequent great relative length of the posterior limbs, which grow disproportionately fast in childhood as compared with the anterior, makes progression on them more rapid by giving a longer stride and at the same time makes it almost impossible to go on " all fours " except by crawling on the hands and knees. In other Primates this disproportion between the anterior and posterior limbs does not occur to nearly the same extent.

In man the skull is nearly balanced on the top of the vertebral column, the occipital condyles which articulate with the atlas being about its middle (Fig. 30), so that but little effort is needed to keep the head erect. In four-footed beasts, on the contrary, the skull is carried on the front end of the horizontal vertebral column and needs special ligaments to sustain it. For instance, in the ox and sheep there is a great elastic cord running from the cervical vertebræ to the back of the skull and helping to hold up the head. Even in the highest apes the skull does not balance on the top of the spinal column; the face part is much heavier than the back, while in man the face parts are relatively smaller and the cranium larger, so that the two nearly equipoise. To keep the head erect and look things straight in the face, "like a man,"

is for the apes far more fatiguing, and so they cannot long maintain that position.

The human spinal column, gradually widening from the neck to the sacrum, is well fitted to sustain the weight of the head, upper limbs, etc., carried by it; and its curvatures, which are peculiarly human, give it considerable elasticity combined with strength. The pelvis, to the sides of which the lower limbs are attached, is proportionately very broad in man, so that the balance can be more readily maintained during lateral bending of the trunk. The arched instep and broad sole of the human foot are also very characteristic. The majority of four-footed beasts, as horses, walk on the tips of their toes and fingers; and those animals, as bears and apes, which like man place the tarsus also on the ground, or in technical language are *plantigrade*, have a much less marked arch there. The vaulted human tarsus, composed of a number of small bones, each of which can glide a little over its neighbors, but none of which can move much, is admirably calculated to break any jar which might be transmitted to the spinal column by the contact of the sole with the ground at each step. A well-arched instep is therefore rightly considered a beauty; it makes progression easier, and by its springiness gives elasticity to the step. In London flat-footed candidates for appointment as policemen are rejected, as they cannot stand the fatigue of walking the daily "beat."

CHAPTER VII.

THE STRUCTURE AND COMPOSITION OF BONE. JOINTS.

Gross Structure of the Bones. The bones of the Body have all a similar structure and composition, but on account of differences in shape they are divided by anatomists into the following groups: (1) *Long bones*, more or less cylindrical in form, like the bones of the thigh and arm, leg and forearm, metacarpus, metatarsus, fingers and toes. (2) *Tabular bones*, in the form of expanded plates, like the bones on the roof and sides of the skull, and the shoulder-blades. (3) *Short bones*, rounded or angular in form and not much greater in one diameter than in another, like the bones of the tarsus and carpus. (4) *Irregular bones*, including all which do not fit well into any of the preceding groups, and commonly lying in the middle line of the Body and divisible into similar halves, as the vertebræ. Living bones have a bluish-white color and possess considerable elasticity, which is best seen in long slender bones such as the ribs.

To get a general idea of the structure of a bone, we may select the humerus for examination. Externally in the fresh state it is covered by a dense white fibrous membrane very closely adherent to it and containing many small blood-vessels. This membrane is the *periosteum;* on its under side new osseous tissue is formed while the bone is still growing, and all through life it is concerned in maintaining the nutrition of the bone, which dies if it be stripped off. The periosteum covers the whole surface of the bone except its ends in the elbow and shoulder joints; the surfaces there which come into contact with other bones and glide over them in the movements of the joint have no periosteum, but are covered by a thin layer of gristle, known as the articular cartilage. Very early in the development of the Body the bone in fact was represented entirely by cartilage; but afterwards nearly all this was replaced by osseous tissue, leaving only a thin cartilaginous layer at the ends.

The bone itself, Fig. 39, consists of a central nearly cylindrical portion or *shaft*, extending between the dotted lines *x* and *z* in the figure, and two enlarged *articular extremities.*

$\frac{1}{3}$
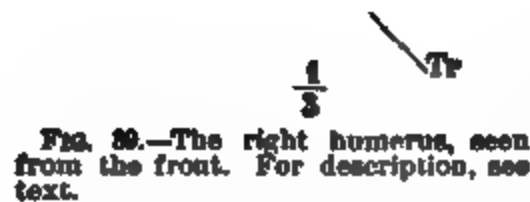
Fig. 39.—The right humerus, seen from the front. For description, see text.
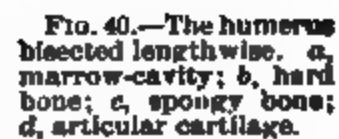
Fig. 40.—The humerus bisected lengthwise. *a*, marrow-cavity; *b*, hard bone; *c*, spongy bone; *d*, articular cartilage.

On the upper articular extremity is the rounded surface, *Cp,* which enters into the shoulder-joint, fitting against the

glenoid cavity of the scapula; and on the lower are the simi-
lar surfaces, *Cpl* and *Tr*, which articulate with the radius and
ulna respectively. Besides carrying the articular surfaces,
each extremity presents several prominences. On the upper
are those marked *Tmj* and *Tm* (the *greater* and *smaller tro-
chanters*), which give attachment to muscles; and similar
eminences, the *external* and *internal condyles*, *El* and *Em*,
are seen on the lower end. Besides these, several bony ridges
and rough patches on the shaft indicate places to which mus-
cles of the arm were fixed.

Internal Structure. If the bone be divided longitudinally,
it will be seen that its shaft is hollow, the space being known
as the *medullary cavity*, and in the fresh bone filled with
marrow. Fig. 40 represents such a longitudinal section. It
will be seen that the marrow-cavity does not reach into the ar-
ticular extremities, but that there the bone has a loose spongy
texture, except a thin layer on the surface. In the shaft, on
the other hand, the outer compact layer is much the thicker,
the spongy or *cancellated bone* forming only a thin stratum
immediately around the medullary cavity. To the naked
eye the cancellated bone appears made up of a trellis-work of
thin bony plates which intersect in all directions and sur-
round cavities rather larger than the head of an ordinary
pin; the compact bone, on the contrary, appears to have no
cavities in it until it is examined with a magnifying-glass.
In the spaces of the spongy portion lies, during life, a sub-
stance known as the *red marrow*, which is quite different from
the yellow fatty marrow lying in the central cavity of the
shaft.

Microscopic Structure of Bone. The microscope shows
that the compact bone contains cavities and only differs from
the spongy portion in the fact that these are much smaller,
and the hard true bony plates surrounding them much more
numerous in proportion than in the spongy parts. If a
thin transverse section of the shaft of the humerus be
examined (Fig. 41) with a microscope magnifying twenty
diameters, it will be seen that numerous openings exist all
over the compact parts of the section and gradually become
larger as this passes into the cancellated part, next the medul-
lary cavity. These openings are the cross-sections of tubes
known as the *Haversian canals*, which ramify all through the
bone, running mainly in the direction of its long axis, but

united by numerous cross or oblique branches as seen in the
longitudinal section (Fig. 42). The outermost ones open on
the surface of the bone beneath the periosteum, and in the
living bone blood-vessels run from this through the Haversian
canals and convey materials for its growth and nourishment.

Fig. 41.—*A*, a transverse section of the ulna, natural size; showing the medullary
cavity. *B*, the more deeply shaded part of *A* magnified twenty diameters.

The average diameter of the Haversian canals is 0.05 mm.
($\frac{1}{500}$ of an inch).

Around each Haversian canal lies a set of plates, or *lamellæ*,
of hard bony substance (see the transverse section Fig. 41),
each canal with its lamellæ forming an *Haversian system:*
and the whole bone is made up of a number of such systems,
with the addition of a few lamellæ lying in the corners be-
tween them, and a certain number which run around the
whole bone on its outer and inner surfaces. In the spongy

parts of the bone the Haversian canals are very large and the intervening lamellæ few in number.

Between the lamellæ lie small cavities, the *lacunæ*, each of which is lenticular in form, somewhat like the space which would be inclosed by two watch-glasses joined by their edges. From the lacunæ many extremely fine branching canals, the *canaliculi*, radiate and penetrate the bony lamellæ in all directions. The innermost canaliculi of each system open into the central Haversian canal; and those of various lacunæ intercommunicating, these fine tubes form a set of passages through which liquid which has transuded from the blood-vessels in the Haversian canals can ooze all through the bone. The lacunæ and canaliculi are shown in Fig. 42.

FIG. 42.—A thin longitudinal section of bone, magnified about 350 diameters. *aa*, Haversian canals.

In the living bone a granular nucleated cell lies in each lacuna. These cells, or *bone-corpuscles*, are the remnants of those which built up the bone, the hard parts of the latter being really an intercellular substance or skeleton formed around and by these cells, much in the same way as a calcareous skeleton is formed around a Foraminifer by the activity of its protoplasm. By the co-operation of all the bone-corpuscles, and the union of their skeletons, the whole bone is built up.

In other bones we find the same general arrangement of the parts, an outer dense layer and an inner spongy portion. In the flat and irregular bones there is no medullary cavity, and the whole centre is filled up with cancellated tissue with red marrow in its spaces. For example, in the thin bones roofing in the skull we find an outer and an inner hard layer of compact bone known as the *outer* and *inner table* respectively, the inner especially being véry dense. Between the two tables lies the spongy bone, red in color to the naked eye from the marrow within it, and called the *diploë*. The interior of the vertebræ also is entirely occupied by spongy bone. Everywhere, except where a bone joins some other part of the skeleton, it is covered by the periosteum.

Chemical Composition of Bone. Apart from the bone-corpuscles and the soft contents of the Haversian canals and

of the spaces of the cancellated bone, the bony substance proper, as found in the lamellæ, is composed of earthy and organic portions intimately combined, so that the smallest distinguishable portion of bone contains both. The earthy matters form about two thirds of the total weight of a dried bone, and may be removed by soaking the bone in dilute hydrochloric acid. The organic portion left after this treatment constitutes a flexible mass, retaining the form of the original bone; it consists chiefly of an albuminoid, *ossein*, which by long boiling, especially under pressure at a higher temperature than that at which water boils when exposed freely to the air, is converted into *gelatin*, which dissolves in the hot water. Much of the gelatin of commerce is prepared in this manner by boiling the bones of slaughtered animals, and even well-picked bones may be used to form a good thick soup if boiled under pressure in a Papin's digester; much nutritious matter being, in the common modes of domestic cooking, thrown away in the bones.

The earthy salts of bone may be obtained free from organic matter by calcining a bone in a clear fire, which burns away the organic matter. The residue forms a white very brittle mass, retaining perfectly the shape and structural details of the original bone. It consists mainly of normal calcium phosphate, or *bone-earth* ($Ca_3, 2PO_4$); but there is also present a considerable proportion of calcium carbonate ($CaCO_3$) and smaller quantities of other salts.

Hygiene of the Bony Skeleton. In early life the bones are less rigid, from the fact that the earthy matters then present in them bear a less proportion to the softer organic parts. Hence the bones of an aged person are more brittle and easily broken than those of a child. The bones of a young child are in fact tolerably flexible and may be distorted by any continued strain; therefore children should never be kept sitting for hours, in school or elsewhere, on a bench which is so high that the feet are not supported. If this be insisted upon (for no child will continue it voluntarily) the thigh-bones will almost certainly be bent over the edge of the seat by the weight of the legs and feet, and a permanent distortion may be produced. For the same reason it is important that a child be made to sit straight while writing, to avoid the risk of producing a lateral curvature of the spinal column. The facility with which the bones may be moulded by prolonged

pressure in early life is well seen in the distortion of the feet of Chinese ladies, produced by keeping them in tight shoes; and in the extraordinary forms which some races of man produce in their skulls, by tying boards on the heads of the children.

Throughout the whole of life, moreover, the bones remain among the most easily modified parts of the Body ; although judging from the fact that dead bones are the most permanent parts of fossil animals we might be inclined to think otherwise. The living bone, however, is constantly undergoing changes under the influence of the protoplasmic cells imbedded in it, and in the living Body is constantly being absorbed and reconstructed. The experience of physicians shows that any continued pressure, such as that of a tumor, will cause the absorption and disappearance of bone almost quicker than that of any other tissue; and the same is true of any other continued pressure. Moreover, during life the bones are eminently plastic; under abnormal pressures they are found to quickly assume abnormal shapes, being absorbed and disappearing at points where the pressure is most powerful, and increasing at other points; tight lacing may in this way produce a permanent distortion of the ribs.

When a bone is fractured a surgeon should be called in as soon as possible, for once inflammation has set in and the parts have become swollen it is much more difficult to place the broken ends of the bone together in their proper position than before this has occurred. Once the bones are replaced they must be held in position by splints or bandages, or the muscles attached to them will soon displace them again. With rest, in young and healthy persons complete union will commonly occur in three or four weeks; but in old persons the process of healing is slower and is apt to be imperfect.

Articulations. The bones of the skeleton are joined together in very various ways; sometimes so as to admit of no movement at all between them; in other cases so as to permit only a limited range or variety of movement; and elsewhere so as to allow of very free movement in many directions. All kinds of unions between bones are called *articulations.*

Of articulations permitting no movements, those which

unite the majority of the cranial bones afford a good example. Except the lower jaw, and certain tiny bones inside the temporal bone belonging to the organ of hearing, all the skull-bones are immovably joined together. This union in most cases occurs by means of toothed edges which fit into one another and form jagged lines of union known as *sutures.* Some of these can be well seen in Fig. 29 between the frontal and parietal bones (*coronal suture*) and between the parietal and occipital bones (*lambdoidal suture*); while another lies along the middle line in the top of the crown between the two parietal bones, and is known as the *sagittal suture.* In new-born children where the sagittal meets the coronal and lambdoidal sutures there are large spaces not yet covered in by the neighboring bones, which subsequently extend over them. These openings are known as *fontanelles.* At them a pulsation can often be felt synchronous with each beat of the heart, which, driving more blood into the brain, distends it and causes it to push out the skin where bone is absent. Another good example of an articulation admitting of no movement is that between the rough surfaces on the sides of the sacrum and the innominate bones.

We find good examples of the second class of articulations —those admitting of a slight amount of movement—in the vertebral column. Between every pair of vertebræ from the second cervical to the sacrum is an elastic pad, the *intervertebral disk*, which adheres by its surfaces to the bodies of the vertebræ between which it lies, and only permits so much movement between them as can be brought about by its own compression or stretching. When the back-bone is curved to the right, for instance, each of the intervertebral disks is compressed on its right side and stretched a little on its left, and this combination of movements, each individually but slight, gives considerable flexibility to the spinal column as a whole.

Joints. Articulations permitting of movement by the gliding of one bone over another are known as *joints,* and all have the same fundamental structure, although the amount of movement permitted in different joints is very different.

Hip-joint. We may take this as a good example of a true joint permitting a great amount and variety of movement. On the os innominatum is the cavity of the *acetabulum* (Fig. 43), which is lined inside by a thin layer of *articular carti-*

lage which has an extremely smooth surface. The bony cup is also deepened a little by a cartilaginous rim. The proximal end of the femur consists of a nearly spherical smooth *head,* borne on a somewhat narrower *neck*, and fitting into the acetabulum. This head also is covered with articular cartilage; and it rolls in the acetabulum like a ball in a socket. To keep the bones together and limit the amount of movement, *ligaments* pass from one to the other. These are composed of white fibrous connective tissue (Chap. VIII) and are extremely pliable, but quite inextensible and very strong and

Fig. 43.—Section through the hip-joint.

tough. One is the *capsular ligament*, which forms a sort of loose bag all round the joint, and another is the *round ligament*, which passes from the acetabulum to the head of the femur. Should the latter rotate above a certain extent in its socket, the round ligament and one side of the capsular ligament are put on the stretch, and any further movement which might *dislocate* the femur (that is, remove the head from its socket) is checked. Covering the inside of the capsular ligament and the outside of the round ligament is a layer of flat cells, which are continued in a modified form over the articular cartilages and form the *synovial membrane.* This, which thus forms the lining of the joint, is always

moistened in health by a small quantity of glairy *synovial fluid*, something like the white of a raw egg in consistency, and playing the part of the oil with which the contiguous moving surfaces of a machine are moistened; it makes all run smoothly with very little friction.

In the natural state of the parts, the head of the femur and the bottom and sides of the acetabulum lie in close contact, the two synovial membranes rubbing together. This contact is not maintained by the ligaments, which are too loose and serve only to check excessive movement, but by the numerous stout muscles which pass from the thigh to the trunk and bind the two firmly together. Moreover, the atmospheric pressure exerted on the surface of the Body and transmitted through the soft parts to the outside of the air-tight joint helps also to keep the parts in contact. If all the muscles and ligaments around the joint be cut away, it is still found in the dead Body that the head of the femur will be kept in its socket by this pressure, and so firmly as to bear the weight of the whole limb without dislocation, just as the pressure of the air will enable a boy's " sucker " to lift a tolerably heavy stone.

Ball-and-socket Joints. Such a joint as that at the hip is called a ball-and-socket joint and allows of more free movement than any other. Through movements occurring in it the thigh can be *flexed*, or bent so that the knee approaches the chest; or *extended*, that is, moved in the opposite direction. It can be *abducted*, so that the knee moves outwards; and *adducted*, or moved back towards the other knee again. The limb can also by movements at the hip-joint be *circumducted*, that is, made to describe a cone of which the base is at the foot and the apex at the hip. Finally, *rotation* can occur in the joint, so that with knee and foot joints held rigid the toes can be turned in or out, to a certain extent, by a rolling around of the femur in its socket.

At the junction of the humerus with the scapula is another ball-and-socket joint permitting all the above movements to even a greater extent. This greater range of motion at the shoulder-joint depends mainly on the shallowness of the glenoid cavity as compared with the acetabulum, and upon the absence of any ligament answering to the round ligament of the hip-joint. Another ball-and-socket joint exists between the carpus and the metacarpal bone of the thumb; and others

with the same variety, but a much less range, of movement between each of the remaining metacarpal bones and the proximal phalanx of the finger which articulates with it.

Hinge-joints. Another form of synovial joint is known as a *hinge-joint*. In it the articulating bony surfaces are of such shape as to permit of movement, to and fro, in one plane only, like a door on its hinges. The joints between the phalanges of the fingers are good examples of hinge-joints. If no movement be allowed where the finger joins the palm of the hand it will be found that each can be bent and straightened at its own two joints, but not moved in any other way. The knee is also a hinge-joint, as is the articulation between the lower jaw and the base of the skull which allows us to open and close our mouths. The latter is, however, not a perfect hinge-joint, since it permits of a small amount of lateral movement such as occurs in chewing, and also of a gliding movement by which the lower jaw can be thrust forward so as to protrude the chin and bring the lower row of teeth outside the upper.

Pivot-joints. In this form one bone rotates around another which remains stationary. We have a good example of it between the first and second cervical vertebræ. The first cervical vertebra or *atlas* (Fig. 22) has a very small body and a very large arch, and its neural canal is subdivided by a transverse ligament (*L*, Fig. 22) into a dorsal and a ventral portion; in the former the spinal cord lies. The second vertebra or *axis* (Fig. 23) has arising from its body the stout bony peg, *D*, called the *odontoid process*. This projects into the ventral portion of the space surrounded by the atlas, and, kept in place there by the transverse ligament, forms a pivot around which the atlas, carrying the skull with it, rotates when we turn the head from side to side. The joints on each side between the atlas and the skull are hinge-joints and permit only the movements of nodding and raising the head. When the head is leaned over to one side, the cervical part of the spinal column is bent.

Another kind of pivot-joint is seen in the forearm. If the limb be held straight out, with the palm up and the elbow resting on the table, so that the shoulder-joint be kept steady while the hand is rotated until its back is turned upwards, it will be found that the radius has partly rolled round the ulna. When the palm is upwards and the thumb outwards, the

lower end of the radius can be felt on the outer side of the forearm just above the wrist, and if this be done while the hand is turning over, it will be easily discerned that during the movement this end of the radius, carrying the hand with it, travels around the lower end of the ulna so as to get to its inner side. The relative position of the bones when the palm is upwards is shown at A in Fig. 44, and when the palm is down at B. The former position is known as *supination ;* the latter as *pronation.* The elbow end of the humerus (Fig. 39) bears a large articular surface: on the inner two thirds of this, *Tr,* the ulna fits, and the ridges and grooves of both bones interlocking form a hinge-joint, allowing only of bending or straightening the forearm on the arm. The radius fits on the rounded outer third, *Cpl,* and forms there a ball-and-socket joint at which the movement takes place when the hand is turned from the supine to the prone position; the ulna forming a fixed bar around which the lower end of the radius is moved.

B   A

Fig. 44.—A, arm in supination; B, arm in pronation. *H,* humerus; *R,* radius; *U,* ulna.

Gliding Joints. These permit as a rule but little movement: examples are found between the closely packed bones of the tarsus (Fig. 38) and carpus, which slide a little over one another when subjected to pressure.

Hygiene of the Joints. When a bone is displaced or *dislocated* the ligaments around the joint are more or less torn and other soft parts injured. This soon leads to inflammation and swelling which make not only the recognition of the injury but, after diagnosis, the replacement of the bone, or the *reduction of the dislocation,* difficult. Moreover the muscles attached to it constantly pull on the displaced bone and drag it still farther out of place; so that it is of great importance that a dislocation be reduced as soon as possible. In most cases this can only be attempted with safety by one

who knows the form of the bones, and possesses sufficient anatomical knowledge to recognize the direction of the displacement. No injury to a joint should be neglected. Inflammation once started there is often difficult to check and runs on, in a chronic way, until the synovial surfaces are destroyed, and the two bones perhaps grow together, rendering the joint permanently stiff. A sprained joint should get immediate and complete rest, for weeks if necessary, and if there be much swelling, or continued pain, medical advice should be obtained. An improperly cared-for sprain is the cause of many a useless ankle or knee.

CHAPTER VIII.

CARTILAGE AND CONNECTIVE TISSUE.

Temporary and Permanent Cartilages. In early life a great many parts of the supporting framework of the Body, which afterwards become bone, consist of cartilage. Such for example is the case with all the vertebræ, and with the bones of the limbs. In these cartilages subsequently the process known as *ossification* takes place, by which a great portion of the original cartilaginous model is removed and replaced by true osseous tissue. Often, however, some of the primitive cartilage is left throughout the whole of life at the ends of the bones in joints where it forms the articular cartilages; and in various other places still larger masses remain, such as the costal cartilages, those in the external ears forming their framework, others finishing the skeleton of the nose which is only incompletely bony, and many in internal parts of the Body, as the cartilage of "Adam's apple," which can be felt in the front of the neck, and a number of rings around the windpipe serving to keep it open. These persistent masses are known as the *permanent*, the others as the *temporary cartilages.* In old age many so-called permanent cartilages become *calcified*—that is, hardened and made unyielding by deposits of lime-salts in them—without assuming the histological character of bone, and this calcification of the permanent cartilages is one chief cause of the want of pliability and suppleness of the frame in advanced life.

Hyaline Cartilage. In its purest form cartilage is flexible and elastic, of a pale bluish-white color when alive and seen in large masses, and cuts readily with a knife. In thin pieces it is quite transparent. Everywhere except in the joints it is invested by a tough adherent membrane, the *perichondrium*, which resembles in structure and function the periosteum of the bones. When boiled for a long time in water, such cartilages yield a solution of *chondrin*, which differs from gelatin in minor points, but agrees with it in the fact that its solution in hot water "sets" or gelatinizes on cool-

ing. When a thin slice of hyaline cartilage is examined with a microscope it is found (Fig. 45) to consist of granular nucleated cells, often collected into groups of two, four, or more, scattered through a homogeneous or faintly granular ground-substance or *matrix*. Essentially, cartilage resembles bone, being made up of protoplasmic cells and a proportionately large amount of non-protoplasmic intercellular substance, the

FIG. 45.—A thin slice of cartilage, magnified, to show the cells imbedded in the homogeneous matrix. *a*, a cell in which the nucleus has divided; *b*, a cell in which division is just complete; *c, c,* a group of four cells resulting from further division of a pair like *b*; the new cells have formed some matrix between them, separating them from another; *d, d,* cavities in the matrix from which cells have dropped out during the preparation of the specimen.

cells being the more actively living part and the matrix their product. Examples of this *hyaline* variety (so called from its glassy transparent appearance) are found in all the temporary cartilages, and in the costal and articular among the permanent.

Cartilages rarely contain blood-vessels except at points where a temporary cartilage is being removed and replaced by bone; then blood-vessels run in from the perichondrium and form loops in the matrix, around which it is absorbed and bony tissue deposited. In consequence of the usual absence of blood-vessels the nutritive processes and exchanges of material must be small and slow in cartilage, as might indeed be expected from the passive and merely mechanical rôle which this tissue plays.

Hyaline cartilage is the type, or most characteristically developed form, of a tissue found with modifications elsewhere in the Body. One of its other modifications is the so-called *cellular cartilage*, which consists of the cells with hardly any matrix, only just enough to form a thin capsule around each. This form is that with which all the carti-

lages commence, the hyaline variety being built up by the increase of the cell-capsules and their fusion to form the matrix. It persists throughout life in the thin cartilaginous plate of a mouse's external ear. Other varieties of cartilage are really mixtures of true cartilage and connective tissues, and will be considered after the latter.

The Connective Tissues. These complete the skeleton, marked out in its coarser features by the bones and cartilages, and constitute the final group of the supporting tissues. They occur in all forms, from broad membranes and stout cords to the finest threads forming networks around the other ultimate histological elements of various organs. In addition to subsidiary forms, three main varieties of this tissue are readily distinguishable, viz., *areolar, white fibrous,* and *yellow elastic.* Each consists of fibres and cells, the fibres being of two kinds, mixed in nearly equal proportions in the areolar variety, while one kind predominates in one and another in the second of the remaining chief forms.

Areolar Connective Tissue. This exists abundantly beneath the skin, where it forms a loose layer which permits the skin to be moved, more or less, to and fro over the subjacent parts. Areolar tissue consists of innumerable bands and cords interlacing in all directions, and can be greatly distended by blowing air in at any point, from whence it travels widely through the intercommunicating meshes: if dried while distended it is somewhat like raw cotton in appearance but not so white. In dropsy of the legs or feet the cavities of this tissue are distended with lymph, which in health is present only in sufficient quantity to moisten them. From beneath the skin the areolar tissue extends all through the Body between the muscles and around the blood-vessels and nerves; and still finer layers of it enter into these and other organs and unite their various parts together. It constitutes in fact a soft packing material which fills up the holes and corners of the Body, as for instance around the blood-vessels and between the muscles in Fig. 4.

Microscopic Structure of Areolar Tissue. When examined with the microscope areolar tissue is seen to consist of nucleated cells imbedded in a ground-substance which is permeated by fibres. The fibres everywhere form the predominant feature of the tissue (the homogeneous matrix and the cells being inconspicuous) and are of two very different kinds.

In a strict sense indeed the areolar tissue ought to be considered as a mixture of two tissues, one corresponding to each variety of fibres in it. It is characterized by its loose texture and by the fact that the two forms of fibres are present in about equal quantities. In many places a tissue containing the same histological elements as the areolar tissue is found in the form of dense membranes, as for example periosteum and perichondrium.

White Fibrous Tissue. One of the varieties of fibres pervading the matrix of areolar tissue exists almost unmixed with the other kind in the cords or *tendons* which unite mus-

Fig. 46.   Fig. 46a.

Fig. 46.—White fibrous connective tissue, highly magnified. The nucleated corpuscles, seen edgewise and appearing spindle-shaped, are seen here and there on the surface of the bundles of fibres.
Fig. 46a.—Yellow elastic tissue, magnified after its fibres have been torn apart.

cles to the bones. This form, known as the *white fibrous connective tissue,* is also found fairly pure in the ligaments around most joints. Physically it is very flexible but extremely tough and inextensible, so that it will readily bend in any direction but is very hard to break; when fresh it has an opaque white color.

White fibrous tissue (Fig. 46) consists of a matrix, containing cavities in which cells lie, and pervaded by bundles of extremely fine fibres. These fibres run in each bundle toler-

ably parallel to one another in a wavy course (Fig. 46) and never branch or unite. Their diameter varies from 0.0005 to 0.001 millimeter ($\frac{1}{50000}$ to $\frac{1}{25000}$ of an inch).

Chemically this tissue is characterized by the fact that its fibres swell up and become indistinguishable when treated with dilute acetic acid, and by the fact that it yields gelatin when boiled in water. The substance in it, called ossein in bones, which is turned into gelatin by such treatment, is here known as *collagen*. Glue is impure gelatin obtained from tendons and ligaments, and calf's-foot jelly, so often recommended to invalids, is a purer form of the same substance obtained by boiling the feet of calves, which contain the tendons of many muscles passing from the leg to the foot.

Elastic Tissue. This is almost invariably mixed in some proportion in all specimens of white fibrous tissue, even the purest, such as the tendons of muscles; but in certain places it exists almost alone, as for example in the ligaments (*ligamenta subflava*) between the arches of the vertebræ, and in the coats of the larger arteries. In quadrupeds it forms the great ligament already referred to (p. 83), which helps to sustain the head. This tissue, in mass, is of a dull yellow color and extremely extensible and elastic; when purest nearly as much so as a piece of india-rubber. Sometimes it appears under the microscope to be made up of delicate membranes, but more often it is in the form of fibres (Fig. 46a) which are coarser than those of white fibrous tissue and frequently branch and unite. It is unaffected by acetic acid and does not yield gelatin when boiled in water.

Connective-tissue Corpuscles. The fibres of white fibrous tissue, wherever it is found, are united into bundles by a structureless ground-material known as the *cement-substance*, which also invests each bundle, or skein as we may call it, with a delicate coating. In this ground-substance are numerous cavities, branched and flattened in one diameter, and often intercommunicating by their branches. In these cavities lie nucleated masses of protoplasm (Fig. 47), frequently also branched, known as the *connective-tissue corpuscles*. These it is which build up the tissue, each cell in the course of development forming around it a quantity of intercellular substance, which subsequently becomes fibrillated in great part, the remainder forming the cement. The cells do not quite fill the cavities in which they

lie, and these opening into others by their offsets there is formed a set of minute tubes ramifying through the connective tissues; and (since these in turn permeate nearly all the Body) pervading all the organs. In these cell-cavities and their branches the lymph flows before it enters definite lymphatic vessels, and they are accordingly known as *lymph*
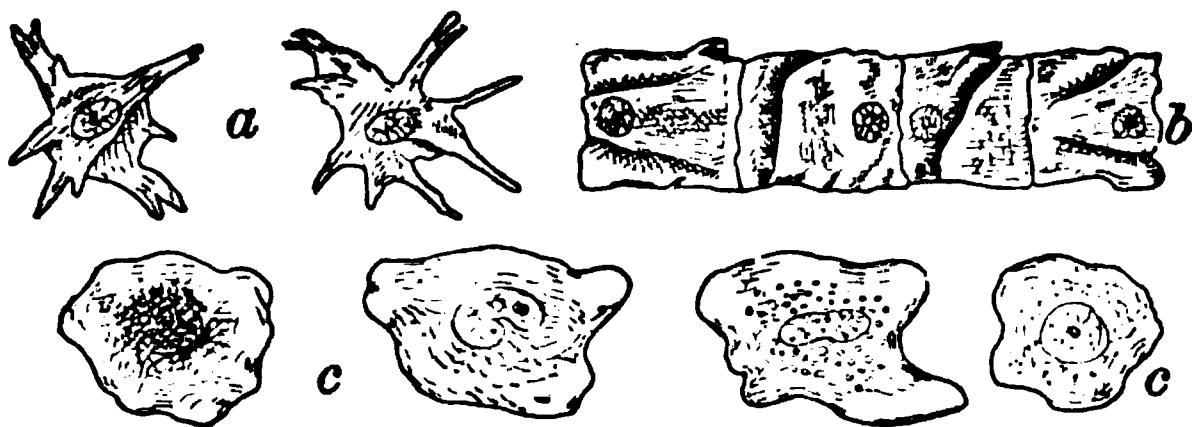
Fig. 47.—Connective-tissue corpuscles : *a*, from areolar tissue ; *b*, from tendon ; *c*, wandering cells.

canaliculi. In addition to the fixed branched connective-tissue corpuscles there are often found other cells, when living connective tissue is examined. These cells much resemble white blood-corpuscles, and probably are such which have bored through the walls of the finer blood-vessels. They creep about along the canaliculi by means of their faculty of amœboid movement, and are known as the "wandering cells."

Subsidiary Varieties of Connective Tissue —In various parts of the Body are connective-tissue structures which have not undergone the typical development, but have departed from it in one way or another. The cells having formed a non-fibrillated intercellular substance around them, development may go no farther and the mass remain permanently as the *jellylike connective tissue ;* or, as in the vitreous humor of the eye (Chap. XXXI), the cells having formed the soft matrix, may disappear and leave the latter only. In other cases the intercellular substance disappears and the cells branching, and joining by the ends of their branches, form a network themselves, nucleated or not at the points answering to the centre of each originally separate cell. This is known as *adenoid* connective tissue. In other cases the cells almost alone constitute the tissue, becoming flattened, closely fitted at their edges, and united by a very small amount of cement-substance. Membranes formed in this way lie beneath epithelium in many places and are known as *basement-*

membranes: the flat cells (Fig. 11, *b*) which form the epithelium of the serous cavities are themselves a layer of modified connective-tissue corpuscles.

In brain and spinal cord, protecting and supporting the nerve-tissues, are found branched cells forming the *neuroglia.* They are not true connective tissue, but correspond to cells of the horny layer of the epidermis, shut in when the medullary canal was closed in the embryo.

Elastic Cartilage and Fibro-cartilage. We may now return to cartilages and consider those forms which are made up of more or less true cartilage mixed with less or more connective tissue of one kind or another. The cartilages of the ear and nose and some others have their matrix pervaded by fine branching fibres of yellow elastic tissue, which form networks around the groups of cartilage-cells. Such cartilages are pliable and tough and possess also considerable extensibility and elasticity. They are known as *elastic* or, from their color, as *yellow cartilages.* Elsewhere, especially in the cartilages which lie between the bones in some joints, we find forms which have the matrix pervaded by white fibrous tissue and known as *fibro-cartilages.* For example the articular cartilage on the end of the lower jaw does not come into

FIG. 48.—Section through the joint of the lower jaw showing its interarticular fibro-cartilage, *x,* with the synovial cavity on each side of it.

direct contact with that covering its socket on the skull, but lying between the two in the joint (Fig. 48) is an *interarticular fibro-cartilage:* similar cartilages exist in the knee-joint;

and the intervertebral disks are also made up of this tissue. Both elastic cartilage and fibro-cartilage often shade off insensibly into pure elastic or pure white fibrous connective tissue.

Homologies of the Supporting Tissues. Bone, cartilage, and connective tissue all agree in broad structural characters, and in the uses to which they are applied in the Body. In each of them the cells which have built up the tissue, with few exceptions, form an inconspicuous part of it in its fully developed state, the chief mass of it consisting of intercellular substance. In hyaline cartilages this latter is not fibrillated; but these cartilages pass insensibly in various regions of the Body into elastic or fibro-cartilages, and these latter in turn into elastic or fibrous connective tissue. The lamellæ of bone, too, when peeled off a bone softened in acid and examined with a very high magnifying power, are seen to be pervaded by fine fibres. Structurally, therefore, one can draw no hard and fast line between these tissues. The same is true of their chemical composition; bone and white fibrous tissue contain a substance (collagen) which is converted into gelatin when boiled in water; and in old people many cartilages become hardened by the deposit in their matrix of the same lime-salts which give its hardness to bone. Further, the developmental history of all of them is much alike. In very early life each is represented by cells only: these form an intercellular substance, and this subsequently may become fibrillated, or calcified, or both. Finally they all agree in manifesting in health no great physiological activity, their use in the Body depending upon the mechanical properties of their intercellular portions.

The close alliance of all three is further shown by the frequency with which they replace one another. All the bones and cartilages of the adult are at first represented only by collections of connective tissue. Before or after birth this is in some cases substituted by bone directly (as in the case of the collar-bone and the bones on the roof of the skull), while in other cases cartilage supplants the connective tissue, to be afterwards in many places replaced by bone, while elsewhere it remains throughout life.

Moreover in different adult animals we often find the same part bony in one, cartilaginous in a second, and composed of connective tissue in a third: so that these tissues

not only represent one another at different stages in the life of the same animal but permanently throughout the whole life of different animals. Low in the animal scale we find them all represented merely by cells with structureless intercellular substance: a little higher in the scale the latter becomes fibrillated and forms distinct connective tissue. In the highest Mollusks (as the cuttle-fishes) this is partly replaced by cartilage, and the same is true of the lowest fishes; while in some other fishes and the remaining Vertebrates we find more or less bone appearing in place of the original connective tissue or cartilage.

From the similarity of their modes of development and fundamental structure, the transitional forms which exist between them, and the frequency with which they replace one another, histologists class the three (bone, cartilage, and connective tissue) together as *homologous tissues* and regard them as differentiations of the same original structure.

Hygienic Remarks. Since in the new-born infant many parts which will ultimately become bone consist only of cartilage, the young child requires food which shall contain a large proportion of the lime-salts which are used in building up bone. Nature provides this in the milk, which is rich in such salts (see Chap. XXI), and no other food can thoroughly replace it. Long after infancy milk should form a large part of a child's diet. Many children though given food abundant in quantity are really starved, since their food does not contain in sufficient amount the mineral salts requisite for their healthy development.

At birth even those bones of a child which are most ossified are often not continuous masses of osseous tissue. In the humerus, for example, the shaft of the bone is well ossified and so is each end, but between the shafts and each of the articular extremities there still remains a cartilaginous layer, and at those points the bone increases in length, new cartilage being formed and replaced by bone. The bone increases in thickness by new osseous tissue formed beneath the periosteum. The same thing is true of the bones of the leg. On account of the largely cartilaginous and imperfectly knit state of its bones, it is cruel to encourage a young child to walk beyond its strength, and may lead to "bow-legs" or other permanent distortions. Nevertheless here as elsewhere in the animal body, moderate exercise promotes the growth of

the tissues concerned, and it is nearly as bad to wheel a child about forever in a baby-carriage as to force it to over exertion.

The best rule is to let a healthy child use its limbs when it feels inclined, but not by praise or blame to incite it to efforts which are beyond its age, and so sacrifice its healthy growth to the vanity of parent or nurse.

The final knitting together of the bony articular ends with the shaft of many bones takes place only comparatively late in life, and the age at which it occurs varies much in different bones. Generally speaking, a layer of cartilage remains between the shaft and the ends of the bone, until the latter has attained its full adult length. To take a few examples : the lower articular extremity of the humerus only becomes continuous with the shaft by bony tissue in the sixteenth or seventeenth year of life. The upper articular extremity only joins the shaft by bony continuity in the twentieth year. The upper end of the femur joins the shaft by bone from the seventeenth to the nineteenth year, and the lower end during the twentieth. In the tibia the upper extremity and the shaft unite in the twenty-first year, and the lower end and the shaft in the eighteenth or nineteenth : while in the fibula the upper end joins the shaft in the twenty-fourth year, and the lower end in the twenty-first. The separate vertebræ of the sacrum are only united to form one bone in the twenty-fifth year of life; and the ilium, ischium, and pubis unite to form the *os innominatum* about the same period. Up to about twenty-five then the skeleton is not firmly "knit," and is incapable, without risk of injury, of bearing strains which it might afterwards meet with impunity. To let lads of sixteen or seventeen row and take other exercise in plenty is one thing, and a good one; but to allow them to undergo the severe and prolonged strain of training for and rowing a long race is quite another, and not devoid of risk.

Adipose Tissue. Fatty substances of several kinds exist in considerable quantity in the Human Body in health, some as minute droplets floating in the bodily liquids or imbedded in various cells, but most in special cells, nearly filled with fat, and collected into masses with supporting and nutritive parts to form *adipose tissue*. In fact almost in every spot where the widely distributed areolar tissue is found, there is adipose tissue in greater or less proportion mixed with it.

Considerable quantities exist for example in the subcutaneous areolar tissue, especially in the female sex, giving the figure of the woman its general more graceful roundness of contour when compared with that of the male. Large quantities commonly lie in the abdominal cavity around the kidneys; in the eye-sockets, forming a pad for the eyeballs; in the marrow of bones; around the joints, and so on.

Examined with the microscope (Fig. 49) adipose tissue is found to consist of small vesicles from 0.2 mm. to 0.09 mm. ($\frac{1}{100}$ to $\frac{1}{300}$ inch) in diameter, clustered together into little masses and bound to one another by connective tissue and blood-vessels which intertwine around

Fig. 49.—Fat-cells imbedded in areolar tissue. *a*, nucleus; *b*, protoplasm; *c*, oil-droplet.

them; in this way the little angular masses which are seen in beef-suet are formed, each mass being separated by a somewhat coarser partition of areolar tissue from its neighbors. The individual fat-cells are spherical or ovoid except when closely packed; then they become polygonal. Each consists of a delicate envelope containing oily matter, which in life is liquid at the temperature of the Body. Besides the oily matter, a nucleus is commonly present in each fat-cell; and a thin layer of protoplasm, exaggerated in Fig. 49, forms a lining to the cell-wall. The oily matter consists of a mixture of palmatin, olein and stearin, which are compounds of palmitic, stearic and oleic acids with glycerin, three molecules of the acid being combined with one of glycerin, with the elimination of water; as for example:

$$3\left(\begin{matrix}C_{18}H_{35}O \\ H\end{matrix}\right\} O\right) + \begin{matrix}C_3H_5 \\ H_3\end{matrix}\right\} O_3 = \begin{matrix}3(C_{18}H_{35}O) \\ C_3H_5\end{matrix}\right\} O_3 + 3H_2O$$

Stearic acid.　　　Glycerin.　　　Stearin.　　　Water.

CHAPTER IX.

THE STRUCTURE OF THE MOTOR ORGANS.

Motion in Animals and Plants. If one were asked to point out the most distinctive property of living animals, the answer would probably be, their power of executing spontaneous movements. Animals as wc commonly know them are rarely at rest, while trees and stones move only when acted upon by external forces, which are in most cases readily recognizable. Even at their quietest times some kind of motion is observable in the higher animals. In our own Bodies during the deepest sleep the breathing movements and the beat of the heart continue; their cessation is to an onlooker the most obvious sign of death. Here, however, as elsewhere in Biology, we find that precise boundaries do not exist; at any rate so far as animals and plants are concerned we cannot draw a hard and fast line between them with reference to the presence or absence of apparently spontaneous motility. Many a flower closes in the evening to expand again in the morning sun; and in many plants comparatively rapid and extensive movements can be called forth by a slight touch, which in itself is quite insufficient to produce mechanically that amount of motion in the mass. The Venus's flytrap (*Dionœa muscipula*) for example has fine hairs on its leaves, and when these are touched by an insect the leaf closes up so as to imprison the animal, which is subsequently digested and absorbed by the leaf. The higher plants it is true have not the power of *locomotion*, they cannot change their place as the higher animals can; but on the other hand some of the lower animals are permanently fixed to one spot; and among the lowest plants many are known which swim about actively through the water in which they live. The lowest animals and plants are in fact those which have undergone least differentiation in their development, and which therefore resemble each other in possessing, in a more or less manifest degree, all the fundamental physiological properties of that simple mass of

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protoplasm which formed the starting-point of each individual. With the physiological division of labor which takes place in the higher forms we find that, speaking broadly, plants especially develop nutritive tissues, while animals are characterized by the high development of tissues with motor and irritable properties; so that the preponderance of these latter is very marked when a complex animal, like a dog or a man, is compared with a complex plant, like a pine or a hickory. The higher animal possesses in addition to greatly developed nutritive tissues (which differ only in detail from those of the plant, and constitute what are therefore often called *organs of vegetative life*) well-developed spontaneous, irritable and contractile tissues, found mainly in the nervous and muscular systems, and forming what have been called the *organs of animal life*. Since these place the animal in close relationship with the surrounding universe, enabling slight external forces to excite it, and it in turn to act upon external objects, they are also often spoken of as *organs of relation*. In man they have a higher development on the whole than in any other animal, and give him his leading place in the animate world, and his power of so largely controlling and directing natural forces for his own good, while the plant can only passively strive to endure and make the best of what happens to it; it has little or no influence in controlling the *happening*.

Amœboid Cells. The simplest motor tissues in the adult Human Body are the amœboid cells (Fig. 15) already described, which may be regarded as the slightly modified descendants of the undifferentiated cells which at one time made up the whole Body. In the adult they are not attached to other parts, so that their changes of form only affect themselves and produce no movements in the rest of the Body. Hence with regard to the whole frame they can hardly be called motor tissues, and are classed in the group of *undifferentiated tissues*.

Ciliated Cells. As the growing Body develops from its primitive simplicity we find that the cells lining some of the tubes and cavities in its interior undergo a very remarkable change, by which each cell differentiates itself into a nutritive and a highly motile and spontaneous portion. Such cells are found for example lining the windpipe, and are represented in Fig. 50. Each has a conical form, the base of the cone being turned to the cavity of the air-tube, and con-

tains an oval nucleus with a nucleolus. On the broader free end are a number (about thirty on the average) of extremely fine processes called *cilia*. During life these are in constant rapid movement, lashing to and fro in the liquid which moistens the interior of the passage; and as the cells are very closely packed, a bit of the inner surface of the windpipe, examined with a microscope, looks like a field of wheat or barley when the wind blows over it. Each cilium strikes with

FIG. 50.—Ciliated cells.

more force in one direction than in the opposite, and as this direction of more powerful stroke is the same for all the cilia on any one surface, the resultant effect is that the liquid in which they move is driven one way. In the case of the windpipe for example it is driven up towards the throat, and the tenacious liquid or mucus which is thus swept along is finally coughed or "hawked" up and got rid off, instead of accumulating in the deeper air-passages away down in the chest.

These cells afford an extremely interesting example of the division of physiological employments. Each proceeds from a cell which was primitively equally motile, automatic and nutritive in all its parts. But in the fully developed state the nutritive duties have been especially assumed by the conical cell-body, while the automatic and contractile properties have been condensed, so to speak, in that modified portion of the primitive protoplasmic mass which forms the cilia. These, being supplied with elaborated food by the rest of the cell, are raised above the vulgar cares of life and have the opportunity to devote their whole attention to the performance of automatic movements; which are accordingly far more rapid and precise than those executed by the whole cell before any division of labor had occurred in it.

That the movements depend upon the structure and composition of the cells themselves, and not upon influences reaching them from the nervous or other tissues, is proved by the fact that they continue for a long time in isolated cells, removed and placed in a liquid, as blood-serum, which does not alter their physical constitution. In cold-blooded animals, as turtles, whose constituent tissues frequently retain their individual vitality long after that bond of union has been destroyed which constitutes the life of the whole animal as

distinct from the lives of its different tissues, the ciliated cells in the windpipe have been found still at work three weeks after the general death of the animal.

The Muscles. These are the main motor organs; their general appearance is well known to every one in the lean of butcher's meat. While amœboid cells can only move themselves, and (at least in the Human Body) ciliated cells the layer of liquid with which they may happen to be in contact, the majority of the muscles, being fixed to the skeleton, can, by alterations in their form, bring about changes in the form and position of nearly all parts of the Body. With the skeleton and joints, they constitute pre-eminently the organs of motion and locomotion, and are governed by the nervous system which regulates their activity. In fact skeleton, muscles, and nervous system are correlated parts: the degree of usefulness of any one of them largely depends upon the more or less complete development of the others. Man's highly endowed senses and his powers of reflection and reason would be of little use to him, were his muscles less fitted to carry out the dictates of his will or his joints less numerous or mobile. All the muscles are under the control of the nervous system, but all are not governed by it with the co-operation of will or consciousness; some move without our having any direct knowledge of the fact. This is especially the case with certain muscles which are not fixed to the skeleton but surround cavities or tubes in the Body, as the blood-vessels and the alimentary canal, and by their movements control the passage of substances through them. The former group, or *skeletal muscles*, are also from their microscopic characters known as *striped muscles*, while the latter, or *visceral muscles*, are called *unstriped* or *plain muscles*. The skeletal muscles being generally more or less subject to the control of the will (as for example those moving the limbs) are frequently spoken of as *voluntary*, and the visceral muscles, which change their form independently of the will, as *involuntary*. The heart-muscle forms a sort of intermediate link; it is not directly attached to the skeleton, but forms a hollow bag which drives on the blood contained in it and that quite involuntarily; but in its microscopic structure it resembles somewhat the skeletal voluntary muscles. The muscles of respiration might perhaps be cited as another intermediate group. They are striped skeletal muscles and, as we all know, are to a certain extent

subject to the will; any one can draw a deep breath when he chooses. But in ordinary quiet breathing we are quite unconscious of their working, and even when attention is turned to them the power of control is limited; no one can voluntarily hold his breath long enough to suffocate himself. As we shall see hereafter, moreover, any one or all of the striped muscles of the Body may be thrown into activity independently of or even against the will, as, to cite no other instances, is seen in the "fidgets" of nervousness and the irrepressible trembling of extreme terror; so that the names voluntary and involuntary are not good ones. The functional differences between the two groups depend really more on the nervous connections of each than upon any essential difference in the properties of the so-called voluntary or involuntary muscular tissues themselves.

The Skeletal Muscles. In its simplest form a skeletal muscle consists of a red soft central part, the *belly*, which tapers at each end and there passes into one or more dense white cords which consist almost entirely of white fibrous connective tissue. These terminal cords are called the *tendons* of the muscle and serve to attach it to parts of the bony or cartilaginous skeleton. In Fig. 51 is shown the *biceps muscle* of the arm, which lies in front of the *humerus*. Its fleshy belly is seen to divide above and end there in two tendons, one of which, *Bl*, is fixed to the scapula, while the other, *Bb*, joins the tendon of a neighboring muscle (the *coraco-brachial*, *Cb*), and is also fixed above to the shoulder-blade. Near the elbow-joint the muscle is continued into a single tendon, *B'*, which is fixed to the radius, but gives an offshoot, *B''*, to the connective-tissue membranes lying around the elbow-joint.

The belly of every muscle possesses the power of shortening forcibly under certain conditions. In so doing it pulls upon the tendons, which being composed of inextensible white fibrous tissue transmit the movement to the hard parts to which they are attached, just as a pull at one end of a rope may be made to act upon distant objects to which the other end is tied. The tendons are merely passive cords and are sometimes very long, as for instance in the case of the muscles of the fingers, the bellies of many of which lie away in the forearm.

If the tendons at each end of a muscle were fixed to the

same bone the muscle would clearly be able to produce no movement, unless by bending or breaking the bone; the probable result in such a case would be the tearing of the muscle by its own efforts. In the Body, however, the two ends of a muscle are always attached to different parts, usually two bones, between which more or less movement is permitted, and so when the muscle pulls it alters the relative positions of the parts to which its tendons are fixed. In the great majority of cases a true joint lies between the bones on which the muscle can pull, and when the latter *contracts* it produces movement at the joint. Many muscles even pass over two joints and can produce movement at either, as the biceps of the arm which, fixed at one end to the scapula and at the other to the radius, can move the bones at either the shoulder or elbow joint. Where a muscle passes over an articulation it is nearly always reduced to a narrow tendon; otherwise the bulky bellies lying around the joints would make them extremely clumsy and limit their mobility.

Origin and Insertion of Muscles. Almost invariably that part of the skeleton to which one end of a muscle is

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FIG. 52.—The biceps muscle and the arm-bones, to illustrate how, under ordinary circumstances, the elbow joint is flexed when the muscle contracts.

fixed is more easily moved than the part on which it pulls by its other tendon. The less movable attachment of a muscle is called its *origin*, the more movable its *insertion*. Taking for example the *biceps* of the arm, we find that when the belly of the muscle contracts and pulls on its upper and lower tendons, it commonly moves only the forearm, bending the elbow-joint as shown in Fig. 52. The shoulder is so much more firm that it serves as a fixed point, and so that end is

the origin of the muscle, and the forearm attachment, *P*, the insertion. It is clear, however, that this distinction in the mobility of the points of fixation of the muscle is only relative, for, by changing the conditions, the insertion may become the stationary and the origin the moved point; as for instance in going up a rope "hand over hand." In that case the radial end of the muscle is fixed and the shoulder is moved through space by its contraction.

Different Forms of Muscles. Many muscles of the Body have the simple typical form of a belly tapering to a single tendon at each end as *A*, Fig. 53; but others divide at one end and are called *two-headed* or *biceps* muscles; while some are even three-headed or *triceps muscles.* On the other hand some muscles have no tendon at all at one end, the belly running quite up to the point of attachment; and some have no tendon at either end. In many muscles a tendon runs along one side and the fibres of the belly are attached obliquely to it: such muscles (*B*, Fig. 53) are called *penniform* or featherlike; or a tendon runs obliquely down the middle of the muscle and has the fibres of the belly fixed obliquely on each side of it (*C*, Fig. 53), forming a *bipenniform muscle :* or even two tendons may run down the belly and so form a *tripenniform muscle.* In a few cases a tendon is found in the middle of the belly as well as at each end of it; such muscles are called *digastric.* A muscle of this form (Fig. 54) is found in connection with the lower jaw. It arises by a tendon attached to the base of the skull; from there its first belly runs downwards and forwards to the neck by the side of the hyoid bone, where it ends in a tendon which passes through a loop serving as a pulley. This is succeeded by a second belly directed upwards towards the chin, where it ends in a tendon inserted into the lower jaw. Running along the front of the abdomen from the pelvis to the chest is a long muscle on each side of the middle line called the *rectus abdominis:* it is *polygastric,* consisting of four bellies separated by short tendons. Many muscles moreover are not rounded but form wide flat masses,

FIG. 53. Diagrams illustrating typical muscle with a central belly and two terminal tendons. *b,* a penniform muscle; *c,* a bipenniform muscle.

FIG. 54.—A digastric muscle.

as for example the muscle *Ss* seen on the ventral side of the shoulder-blade in Fig. 51.

Gross Structure of a Muscle. However the form of the skeletal muscles and the arrangement of their tendons may vary, the essential structure of all is the same. Each consists of a proper *striped muscular tissue*, which is its essential part, but which is supported by connective tissue, nourished by blood-vessels and lymphatics, and has its activity governed by nerves; so that a great variety of things go to form the complete organ.

A loose sheath of areolar connective tissue, called the *perimysium*, envelops each muscle, and from this partitions run in and subdivide the belly into bundles or *fasciculi* which run from tendon to tendon, or for the whole length of the muscle when it has no tendons. The coarseness or fineness of butcher's meat depends upon the size of these primary fasciculi, which differs in different muscles of the same animal. These larger fasciculi are subdivided by finer connective tissue membranes into smaller ones (as shown in Fig. 55, which represents a few primary fasciculi of a muscle and the secondary fasciculi into which these are divided), each of which consists of a certain number of microscopic *muscular fibres*

Fig. 55.—A small bit of muscle composed of five primary fasciculi. *A*, natural size; *B*, the same magnified three diameters, to show the secondary fasciculi of which the primary are composed.

bound together by very fine connective tissue and enveloped in a close network of blood-vessels. Where a muscle tapers the fibres in the fasciculi become less numerous, and when a tendon is formed disappear altogether, leaving little but the connective tissue.

Histology of Muscle. For the present we need only concern ourselves with the muscular fibres. Each of these is from eight to thirty-five millimetres ($\frac{1}{3}$ to $1\frac{1}{2}$ inches) long, but only from 0.034 to 0.055 mm. ($\frac{1}{750}$ to $\frac{1}{450}$ inch) in diameter in its widest part and tapering to a blunt point at each end. In cross-section the fibres are irregularly polygonal. In long muscles with terminal tendons, no fibre runs the whole length of a fasciculus, which may be a foot or more long, but the

fasciculus is made up of many successive fibres, the narrow end of each fitting in between the ends of those which follow it. In muscles with short fasciculi, the fibres may run the whole length of each of the latter.

The tissue of the skeletal muscles is very easily recognized under the microscope: even when magnified only two or three hundred diameters each fibre is seen to be crossed for its whole width by regularly alternating dimmer and brighter bands (Fig. 56) or stripes. In a relaxed fibre each band is about $\frac{1}{880}$ mm. ($\frac{1}{17000}$ inch) in width, but the brighter bands are a little broader than the darker. In the contracted fibre both kinds of bands become narrower, especially the brighter, and these latter at the same time undergo an optical change and divert the light so that but little of it reaches the eye when the fibre is in focus; in consequence they then look darker than the original dimmer bands lying between them and now appearing as the brighter of the two. A fresh muscle-fibre shows on close examination a faint longitudinal striation. This is much more marked in specimens which have been preserved in alcohol, and these may be teased out into very fine threads which have been named *fibrillæ*.

Fig. 56.—A small part of a muscle-fibre, magnified; showing its cross-striation and a couple of nuclei.

On careful examination each fibre can be made out to possess an external envelope, the *sarcolemma*, enveloping a softer material which makes up the main mass of the fibre; but there are in addition a number of oval nuclei which lie immediately under the sarcolemma and are placed lengthwise in the fibre. On account of its extreme thinness and transparency the sarcolemma cannot be recognized when lying in its natural position, closely applied to the striped contents, but being tougher than these it sometimes remains unbroken when they are crushed and then (Fig. 57) comes into view as an apparently structureless membrane bridging over the gap. The sarcolemma is imperforate except at one point where the central por-
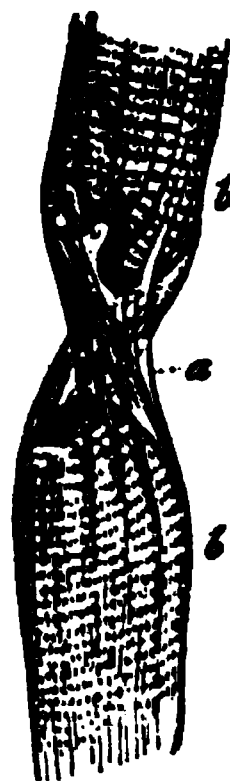
Fig. 57.—A small piece of muscular fibre. At a the fibre has been crushed and twisted so as to tear its contents while the tougher sarcolemma, elsewhere so closely applied to the rest as to be invisible, remains untorn and conspicuous.

tion (or *axis cylinder*, see Chap. XII) of a nerve-fibre penetrates it.

The striped contents which occupy most of the cavity enclosed by the sarcolemma are the essential contractile portion of the fibre and during life are soft or semi-fluid : soon after death they solidify or clot and thus death-stiffening (*rigor mortis*) is produced. At intervals, corresponding to the middle zone of each bright band of the relaxed fibre, an extremely delicate membrane (*membrane of Krause, K,* Fig. 58) crosses the fibre, thus dividing the rest of the contents into a series of disks, each consisting of a dim centre answering

A

B

Fig 58.—Diagrams to illustrate the structure of a small piece of a striped muscle-fibre *A.* in the relaxed, *B,* in the contracted condition; *K, K,* membranes of Krause. *H, H* bands of Hensen; *aa, bb,* parts of sarcostyles, showing their constrictions near Krause's membranes, and the tubulated sarcosomes in each , *c, d, e, f,* a sarcous element; *o,* hyaloplasm; *g,* sarcoplasm.

to the whole of a dark band, and two brighter ends, each corresponding to half of a bright band. Each disk is a *sarcomere.* Under certain conditions, in fact, a fibre may be split up crosswise into a number of such disks. When a fresh muscle-fibre is artificially stretched and examined with a very high magnifying power there may further be made out in the middle of each dim band a transverse line (*band of Hensen, H,* Fig. 58) slightly brighter than the rest of the dim band.

The main bulk of each fibre consists of polygonal rods, the *muscle-columns* or *sarcostyles* (*aa, bb,* Fig. 58), which are inter-

rupted in their course by Krause's membranes. That portion of a sarcostyle, cdef, included between two consecutive membranes is a sarcous element. The terminal portions of each sarcous element are of softer consistence than most of the middle part and correspond to the hyaloplasm (Fig. 7) of a typical primitive cell, and the material composing them may be designated by the same name. The central portion of each sarcous element is mainly made up of a firmer material which stains with hemotoxylin and answers in general to the reticulum of a primitive cell : it is named the sarcous substance or, better, the sarcosome. Each sarcosome is permeated by fine longitudinal tubules which commence at its ends but do not reach to its centre and are thus divided into two sets by a median transverse partition in which the band of Hensen lies. These tubules are filled with hyaloplasm. The sarcous elements are constricted where they abut on Krause's membrane and in consequence each sarcostyle is narrowed at regular intervals along its course. The spaces between the sarcostyles are filled by a very soft sarcoplasm, which is of course more abundant in the regions of Krause's membranes, where the muscle-columns are constricted. In mammalian muscle the sarcoplasm is present in relatively much smaller amount than indicated in Fig. 58. In fresh specimens it can, however, be made out in the form of fine dark lines with swollen ends, lying between contiguous sarcous elements. Gold chloride stains the sarcoplasm deeply but leaves the sarcostyles uncolored : hence in specimens so prepared the edges or ends of the sarcoplastic septa appear as very conspicuous lines, which look, especially in cross-sections, as if due to a network of fibres, as which they have been described by several observers, and been regarded as the essential contractile part of the fibre. In a relaxed muscle-fibre (A, Fig. 58) the sarcosomes are comparatively long and narrow; but during contraction (B) they become shorter and thicker and bulged out in the middle, and more hyaloplasm passes into their tubules, which become distended, especially near their deeper ends : the band of Hensen also ceases to be visible. Contraction of the whole fibre is thus accompanied by or, rather, is due to a transference of hyaloplasm from the ends of each sarcomere into the interior of the sarcosomes of its central portion, in consequence of which the whole fibre becomes shorter and thicker. The swelling of the sarcosome pushes aside some of the

sarcoplasm lying between them and the displaced portion accumulates nearer the ends of the sarcous elements, in the space left by that portion of the hyaloplasm which has entered the tubules: compare *gg* in *A* and *B*, Fig. 58.

Arguing from the analogy of the amœboid cell in which, as we have seen (p. 27), parts consisting only of hyaloplasm can exhibit movements, it would seem probable that in the muscle-fibre the hyaloplasm is to be regarded as the active contractile portion and the sarcosomes as a framework directing the form which the contracted hyaloplasm shall assume, and assuring that it shall be a precise and definite shortening in the direction of the long axis of the fibre with a widening in the transverse direction, instead of such irregular changes of form as are exhibited by the amœboid cell with its irregularly arranged or, sometimes, entirely absent reticulum. That the hyaloplasm and not the sarcoplasm form .the contractile part of the fibre is proved by the fact that in some insect-muscles in which they are unusually large, it is possible to isolate them while alive and observe them still contracting.

The nuclei of the fibres lie in the sarcoplasm, which represents a part of the original protoplasm of the row of cells from which each muscle-fibre develops, that has remained but little changed while the rest was differentiated into sarcous elements.

The blood-vessels and nerve-fibres supplied to the skeletal muscles are numerous. The larger blood-vessels run in the coarser partitions of the connective tissue lying between the fasciculi and give off fine branches which form a network between the individual fibres but never penetrate the sarcolemma.

Connected with each muscle-fibre is a nerve-fibre of the white variety (Chap. XII). The central core of the nerve-fibre ends in an oval expansion (*end plate*) which contains many nuclei and lies close under the sarcolemma, its deeper side being in immediate contact and possibly continuous with the striated contents. These nerve-fibres are *motor* or concerned in exciting a contraction of the muscle-fibre. Other white nerve-fibres are connected with very peculiar bodies found scattered throughout the muscle, but especially numerous near the tendons. They are usually of a size just visible to the unaided eye and from their form have been named *muscle-spindles.* They appear to be sensory in function.

Somewhat similar bodies (Golgi's *tendon-organs*) are found in the tendons and are also richly supplied with nerve-fibres. In histological structure the tendon-organs and the muscle-spindles appear to be allied to Pacinian bodies (Chap. XXXV).

Structure of the Unstriped Muscles. Of these the muscular coat of the stomach (Fig. 59) is a good example.

FIG. 59.—The muscular coat of the stomach.

They have no definite tendons, but form expanded membranes surrounding cavities, so that they have no definite origin or insertion. Like the skeletal muscles they consist of proper contractile elements, with accessory connective tissue, blood-vessels and nerves. Their fibres, however, have a very different microscopic structure. They present a slightly marked longitudinal but no cross striation and are made up of elongated cells (Fig. 60), bound together by a small quantity of cementing material. The cells vary considerably in size, but on the average are about $\frac{1}{24}$ mm. ($\frac{1}{500}$ inch) in length. Each is flattened in one plane, tapers off at each end, and possesses a very thin enveloping membrane; in its interior lies an elongated nucleus with one or two nucleoli. These cells have the

FIG. 60.—Unstriped muscle-cells.

power of shortening in the direction of their long axes, and so of diminishing the capacity of the cavities in the walls of which they lie.

Cardiac Muscular Tissue. This consists of nucleated branched cells which unite to form a network, in the interstices of which blood-capillaries and nerve-fibres run. The cells present transverse striations, but not so distinct as those of the skeletal muscles, and are said to have no sarcolemma.

The Chemistry of Muscular Tissue. The chemical structure of the living muscular fibre is unknown, but some idea as to it may be obtained from examination of the substances it yields on proximate analysis. Muscle contains 75 per cent of water; and, among other inorganic constituents, phosphates and chlorides of potassium, sodium, and magnesium. When at rest a living

Fig. 61.—Cardiac muscular tissue, magnified about 400 diameters. The cell-boundaries and cell-nuclei are indicated only in the right-hand portion of the figure.

muscle is feebly alkaline, but after hard work, or when dying, this reaction is reversed through the formation of sarcolactic acid ($C_3H_6O_3$). Muscles contain small quantities of grape-sugar and glycogen, and of organic nitrogenous crystalline compounds, especially kreatin ($C_4H_9N_3O_2$). As in the case of all other physiologically active tissues, however, the main *post-mortem* constituents of the muscular fibres are proteid substances, and it is probable that like protoplasm itself (p. 27) the essential contractile part of the tissue consists of a complex body containing proteid, carbohydrate and fatty residues; and that during muscular work this is broken up, yielding proteids, carbon dioxide, sarcolactic acid, and probably other things.

During life and for a certain time after general death the muscles are soft, translucent, extensible and elastic, and neutral or feebly alkaline in reaction; after a period which in warm-blooded animals is brief (varying from a few minutes to three or four hours) they gradually become harder, more opaque, less extensible and less elastic, and distinctly acid in reaction. The result of these changes is the well-known cadaveric rigidity or *rigor mortis.* The rigid condition lasts for a day or longer and then it gradually and finally disappears and more marked decomposition changes commence. Until a short time before the commencement of rigor the muscles remain contractile and can be thrown into activity by various

excitants, as electric shocks; that is to say, although the body in general is dead and the beat of the heart and the flow of blood have ceased, yet the muscles retain their vitality for a while. This is especially the case with the muscles of cold-blooded animals, as frogs and turtles, the muscles of which may, especially if kept cool, retain their living properties for several hours after removal from the body of the animal.

If muscles be taken in an early stage of rigor, rapidly freed as much as possible from tendons, fats and connective tissue, and then finely minced and thoroughly washed with water, most of the salts and crystallizable muscle ingredients can be dissolved away, along with a small amount of albumens; but by far the greater part of the albumen is left behind in the form of *myosin*, a proteid which is insoluble in water. On treating the residue with a 10 per cent solution of ammonium chloride the myosin dissolves and may be obtained as a flocculent white precipitate by allowing the solution to fall drop by drop into a large quantity of water, or by adding to it a considerable proportion of common salt. Myosin is related chemically to fibrinogen and globulin, and its solutions in 10 per cent neutral saline are coagulated by heat at the same temperature (56° C. or 158° F.) as the former.

Although myosin is apparently the least altered form in which its chief proteid constituent can be separated from muscle, it does not appear to exist, or at least exists in small quantity if at all, in living muscle; it is an early product of post-mortem chemical changes. Its precursor in living muscle has been named *myosinogen*, and a solution containing that substance may be obtained as follows: Perfectly fresh and still contractile muscles are cut out from a frog which has just been killed by destruction of its brain and spinal cord, a proceeding which entirely deprives the animal of consciousness and the power of using its muscles, but leaves these latter unaltered and alive for some time. The excised muscles are thrown into a vessel cooled below 0° C. by a freezing mixture and are thus frozen hard before any great chemical change has had time to occur in them. The solidified muscles are then cut up into thin slices, the bits thrown on a cooled filter and let gradually warm up to the freezing-point of water, after the addition of some ice-cold 0.5 per cent solution of common salt. Gradually a small quantity of a tenacious alkaline and transparent liquid filters through. This

liquid, known as the *muscle-plasma*, contains myosinogen and like blood-plasma is spontaneously coagulable. It quickly sets into a transparent jelly and this soon separates into *muscle-serum* and *muscle-clot*, the latter consisting of myosin. Dissolved in the muscle-serum are found small quantities of several albumens, one much resembling the serum-albumen of blood. The spontaneous clothing of the plasma, and presumably the natural formation of myosin during rigor mortis, are due to the action on myosinogen of an enzyme, *muscle-ferment*, much resembling fibrin-ferment. The clotting is accompanied by a change of reaction from the alkaline or neutral of the plasma to a markedly acid one: this appears to be mainly due to the formation of sarcolactic acid, the quantity of which bears a proportion to that of the myosin formed, suggesting that both may be products of the breaking-down of a pre-existent more complex substance. It has further been shown that when a muscle passes into the state of rigor it evolves a certain amount of carbon dioxide, and that the quantity of this varies with the quantity of myosin and of sarcolactic acid formed. Hence it has been suggested that in the living muscle there is a substance which after death breaks up yielding (with possibly other things) myosinogen, sarcolactic acid and carbon dioxide; and further that this chemical change is associated with the liberation of energy (Chap. XX) which in the dead muscle is set free mainly as the heat which is known to be evolved by muscles passing into rigor.

The precipitate produced when myosin solutions are heated is coagulated proteid (p. 10) and insoluble in dilute acids and alkalies in which myosin itself is very soluble. When dissolved in dilute acids myosin is converted into *syntonin*, which was formerly supposed to be the chief form of proteid present in dead muscles. Syntonin is insoluble in water and neutral saline solutions, but soluble in dilute acids and alkalies, and its solutions are not coagulated by boiling.

Beef Tea and Liebig's Extract. From the above-stated facts it is clear that when a muscle is boiled in water its myosin is coagulated and left behind in the meat : even if cooking be commenced by soaking in cold water the myosin still remains, as it is as insoluble in cold water as in hot. Beef tea as ordinarily made, then, contains little but the flavoring matters and salts of the meat, traces of some albumens and

some gelatin, the latter derived from the connective tissues of the muscle. The flavoring matters and salts make it deceptively taste as if it were a strong solution of the whole meat, and the gelatin causes it to "set" on cooling, so the cook feels quite sure she has got out "all the strength of the meat," whereas the beef tea so prepared contains but little of the most nutritious proteid portions, which in an insipid shrunken form are left when the liquid is strained off. Various proposals have been made with the object of avoiding this and getting a really nutritive beef tea; as for example chopping the raw meat fine and soaking it in strong brine for some hours to dissolve out the myosin; or extracting it with dilute acids which turn the myosin into syntonin and dissolve it and at the same time render it non-coagulable by heat when subsequently boiled. Such methods, however, make unpalatable compounds which invalids will not take. Beef tea is a slight stimulant, and often extremely useful in temporarily maintaining the strength and in preparing the stomach for other food, but its direct value as a food is slight, and it cannot be relied upon to keep up a patient's strength for any length of time. There can be no doubt that thousands of sick persons have in the past and are being to-day starved to death on it. *Liebig's extract of meat* is essentially a very strong beef tea; containing much of the flavoring substances of the meat, nearly all its salts and the crystalline nitrogenous bodies, such as kreatin, which exist in muscle, but hardly any of its really nutritive parts, as was pointed out by Liebig himself. From its stimulating effects it is often useful to persons in feeble health, but other food should be given with it. It may also be used on account of its flavor to add to the "stock" of soup and for similar purposes ; but the erroneousness of the common belief that it is a highly nutritious food cannot be too strongly insisted upon. Under the name of *liquid extracts of meat* other substances have been prepared by subjecting meat to chemical processes in which it undergoes changes similar to those experienced in digestion: the myosin is thus rendered soluble in water and uncoagulable by heat, and such extracts if properly prepared are nutritious and can often be absorbed when meat in the solid form cannot be digested: they may thus help the stomach over a crisis, but are not, even the best of them, to be depended on as anything but temporary substitutes for other food; or in some cases as useful additions to it.

CHAPTER X.

THE PROPERTIES OF MUSCULAR TISSUE.

Contractility. The characteristic physiological property of muscular tissue, and that for which it is employed in the Body, is the faculty possessed by its fibres of shortening forcibly under certain circumstances. The direction in which this shortening occurs is always that of the long axis of the fibre in both plain and striped muscles, and it is accompanied by an almost equivalent thickening in other diameters, so that when a muscle contracts it does not shrivel up or diminish its bulk in any appreciable way; it simply changes its form. When a muscle contracts it also becomes harder and more rigid, especially if it has to overcome any resistance. This and the change of form can be well felt by placing the fingers of one hand over the biceps muscle lying in front of the humerus of the other arm. When the muscle is contracted so as to bend the elbow it can be felt to swell out and harden as it shortens. Every schoolboy knows that when he appeals to another to " feel his muscle " he contracts the latter so as to make it thicker and apparently more massive as well as harder. In statues the prominences on the surface indicating the muscles beneath the skin are made very conspicuous when violent effort is represented, so as to indicate that the muscles are in vigorous action. In a muscular fibre we find no longer the slow, irregular, and indefinite changes of form seen in amœboid slightly differentiated cells; they are replaced by a precise, rapid and definite change of form. Muscular tissue represents a group of cells in the bodily community which have taken up the one special duty of executing changes of form, and in proportion as these cells have fewer other things to do, they do that one better. This *contractility* of the muscular fibres may be briefly described as a passage from the state of rest, in which the fibres are long and narrow, into the state of activity, in which they are shorter and thicker: this change is made with considerable force, and thus the mus-

cles move parts attached to their tendons. When the state of activity has passed off the fibres suffer themselves to be extended again by any force pulling upon them, and so regain their resting shape; and since in the living Body almost invariably other parts are put upon the stretch when any muscle contracts, these by their elasticity serve to pull the latter back again to its primitive shape. No muscular fibre is known to have the power of actively expanding after it has contracted: in the active state it forcibly resists extension, but once the contraction is completely over, it suffers itself readily to be pulled back to its resting form. The contracted state lasts always longer, however, than the mere time occupied by the muscle in shortening: as will be seen later, the full state of contraction is gradually attained and gradually disappears.

Irritability. With that modification of the primitive protoplasm of an amœboid embryonic cell which gives rise to a muscular fibre with its great contractility, there goes a loss of other properties. Nearly all spontaneity disappears; muscles are not automatic like primitive protoplasm or ciliated cells; except under certain very special conditions they remain at rest unless excited from without. The amount of external change required to excite the living muscular fibre is, however, very small; muscle tissue is highly *irritable*, a very little thing being sufficient to call forth a powerful contraction. In the living Human Body the exciting force, or *stimulus*, acting upon a muscle is almost invariably a *nervous impulse*, a molecular movement transmitted along the nerve-fibre attached to it, and upsetting the molecular equilibrium of the muscle. It is through the nerves that the will acts upon the muscle-fibre, and accordingly injury to the nerves of a part, as the face or a limb, causes paralysis of its muscles. They may still be there, intact and quite ready to work, but there are no means of sending commands to them, and so they remain idle.

Although a nervous impulse is the natural physiological muscular stimulus it is not the only one known. If a muscle be exposed in a living animal and a slight but sudden tap be given to it, or a hot bar be suddenly brought near it, or an electric shock be sent through it, or a drop of glycerin or of solution of ammonia be placed on it, it will contract; so that in addition to the natural nervous stimulus, muscles are irritable under the influence of mechanical, thermal, electrical, and

chemical stimuli. One condition of the efficacy of each of them is that it shall act with some suddenness; a very slowly increased pressure, even if ultimately very great, or a very slowly raised temperature, or a slowly increased electrical current passed through it, will not excite the muscle; although far less pressure, warmth, or electricity more rapidly applied would stimulate it powerfully. Once an electric current has been set up through a muscle, its steady passage does not act as a stimulus; but a sudden diminution or increase of it does. It may perhaps still be objected that it is not proved that any of these stimuli excite the muscular fibres, and that in all these cases it is possible that the muscle is only excited through its nerves. For the various stimuli named above also excite nerves (see Chap. XIII), and when we apply them to the muscle we may really be acting first upon the fine nerve-endings there, and only indirectly and through the mediation of these upon the muscular fibres. That the muscular fibres have a proper irritability of their own, independently of their nerves, is, however, shown by the action of certain drugs—for example curare, a South American Indian arrow poison. When this substance is introduced into a wound all the striped muscles are apparently poisoned, and the animal dies of suffocation because of the cessation of the breathing movements. But the poison does not really act on the muscles themselves: it kills the muscle-nerves, but leaves the muscle intact; and it has been proved to kill the very endings of the muscle-nerves right down in the muscle-fibres themselves. Yet after its administration we still find that the various non-physiological stimuli referred to above make the muscles contract just as powerfully as before the poisoning, so we must conclude that the muscles themselves are irritable in the absence of all nerve stimuli—or, what amounts to the same thing, when all their nerve-fibres have been poisoned. The experiment also shows that the contractility of a muscle is a property belonging to itself, and that its contracting force is not something derived from the nerves attached to it. The nerve stimulus simply acts like the electric shock or sudden blow and arouses the muscle to manifest a property which it already possesses. The older physiologists observing that muscular paralysis followed when the nervous connection between a muscle and the brain was interrupted, concluded that the nerves gave the muscles the power of contracting.

They believed that in the brain there was a great store of a mysterious thing called *vital spirits,* and that some of this was ejected from the brain along the nerve to the muscle, when the latter was to be set at work, and gave it its working power. We now know that such is not the case, but that a muscle-fibre is a collection of highly irritable material which can have its equilibrium upset in a definite way, causing it to change its shape, under the influence of certain slight disturbing forces, one of which is a nervous impulse; and since in the Body no other kind of stimulus usually reaches the muscles, they remain at rest when their nervous connections are severed. But the muscles paralyzed in this way can still, in the living Body, be made to contract by sending electrical shocks through them. Physiologically, then, muscle is a contractile and irritable, but not an automatic, tissue.

A Simple Muscular Contraction. Most of the details concerning the physiological properties of muscles have been studied on those of cold-blooded animals. A frog's muscle will retain all its living properties for some time after removal from the body of the animal, and so can be experimented on with ease, while the muscles of a rabbit or cat soon die under those circumstances. Enough has, however, been observed on the muscles of the higher animals to show that in all essentials they agree with those of the frog or terrapin.

When a single electric shock is sent through a muscle, the nerves of which have been thrown out of action by curare, it rapidly shortens and then, if a weight be hanging on it, rapidly lengthens again. The whole series of phenomena from the moment of stimulation until the muscle regains its resting form is known as a *simple muscular contraction* or a *"twitch":* it occupies in frog's muscle about one tenth of a second. So brief a movement as this cannot be followed in its details by direct observation, but it is possible to record it and study its phases at leisure. This may be done by firmly fixing the upper tendon of an isolated muscle, *M,* Fig. 62, and attaching the other end at *d* to a lever, *l,* which can move about the fulcrum *f*: the end of the long arm of the lever bears a point, *p,* which scratches on a smooth smoked surface, *S.* Suppose the surface to be placed so that the writing point of the lever is at *a*; if the muscle now contracts it will raise the point of the lever, and a line *ac* will be drawn on the
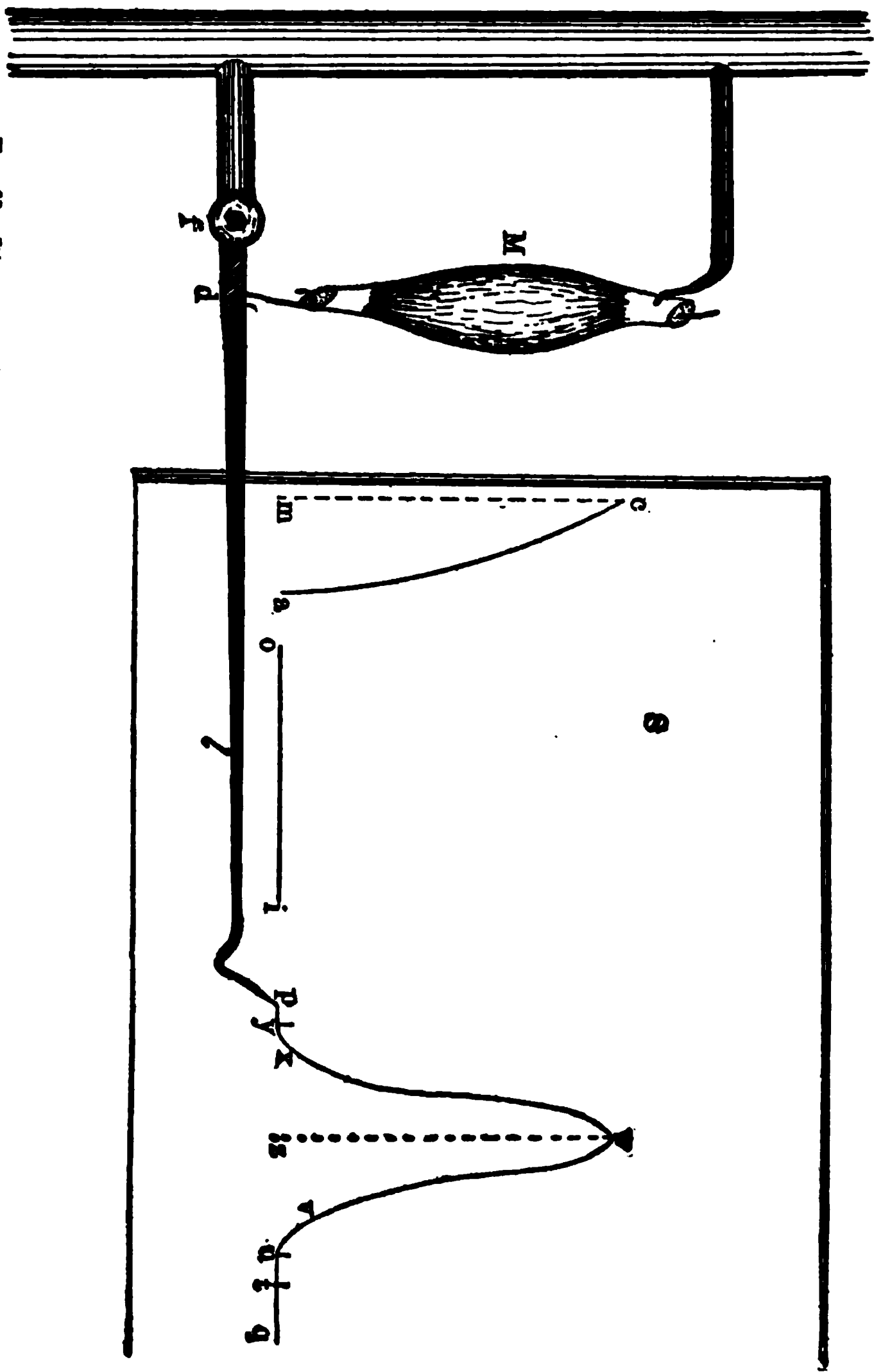
FIG. 62.—Diagram to illustrate the method of obtaining a graphic record of a muscular contraction.

smoked surface, its vertical height, *cm,* being dependent, first, on the extent of the shortening of the muscle, and second, on the proportion between the long and short arms of the lever: the longer *fp* is as compared with *fd,* the more will the actual shortening of the muscle be magnified. With the lever shown in the figure this magnification would be about ten times, so that one tenth of *cm* would be the extent of the shortening of the muscle. Suppose, next, the smoked surface to be moved to such position that the writing point of the lever touches it at *i,* and, the muscle being left at rest, the surface to be moved evenly from left to right; the horizontal line *io* would then be traced, its length depending on the distance through which *S* moved during the time the lever was marking on it: and it is clear that if *S* move uniformly, and we know its rate of movement, we can very readily calculate from the length of *io* how long *S* was moving while that line was being traced: for example, if we know the rate of movement to be ten inches per second, and on measurement find *io* to be an inch long, the time during which the surface was moving must have been $\frac{1}{10}$ of a second; and each tenth of *io* correspond to $\frac{1}{100}$ of a second.

If we set the recording surface in motion and while the lever point is tracing a horizontal line cause the muscle to contract, the point will be raised as long as the muscle is contracted, and the line drawn by it will be due to a combination of two simultaneous movements—a horizontal, due to the motion of *S,* a nearly vertical, due to the shortening of the muscle; the resulting line is a curve known as *the curve of a simple muscular contraction.* Let the surface *S* be placed so that the writing point is at *q* and then be set in uniform motion from left to right at the same rate as before (ten inches per second). When the point is opposite *t,* stimulate the muscle by an electric shock; the result, until the muscle has fully lengthened again, will be the curve *tuvwxy,* from which many things may be learned. In the first place we see that the muscle does not commence to contract at the very instant of stimulation, but at an appreciably later time, and during the interval the lever draws the horizontal line *tu*; this period, occupied by preparatory changes within the muscle, is known as *the period of latent excitation.* Then the muscle begins to shorten and the lever to rise, at first slowly from *u* to *v,* then more rapidly, and again more slowly

until the summit of the contraction is reached at *w*. The muscle does not now instantly relax, but only gradually passes back to the resting state: beginning at *w*, we see the descent of the curve is for a time slow, then more rapid, and finally slow again from *x* to *y*, when the contraction is completed and the lever once more traces only the horizontal line *yp*, due to the continued movement of the recording surface. The curve then shows three distinct phases in the contraction: the period of latent excitation; the period of shortening; the period of elongating. Knowing the rate of horizontal movement, we can measure off the time occupied by each phase. The horizontal distance from *t* to *u* represents the time taken by the latent excitation; from *u* to *z*, the time occupied in shortening; from *z* to *y*, the time taken in elongation: in a fresh frog's muscle these times are respectively $\frac{1}{100}$, $\frac{4}{100}$, $\frac{5}{100}$ of a second. In the muscles of warm-blooded animals they are all shorter, but the difficulties in the way of accurate experiment are very great. If we know the relative lengths of the arms of the lever we can of course readily calculate from the height, *wz*, of the curve the extent of shortening of the muscle. With a single electrical stimulation this is never more than one fourth the total length of the muscle.

In Fig. 62 the accessory apparatus used in practice to indicate on the moving surface the exact instant of stimulation and to measure the rate at which *S* moves have been omitted.

Physiological Tetanus. It is obvious that the ordinary movements of the Body are not brought about by such transient muscular contractions as those just described. Even a wink lasts longer than one tenth of a second. Our movements are, in fact, due to more prolonged contractions which may be described as consisting of several simple contractions fused together, and known as "*tetanic contractions*"; it might be better to call them "compound contractions," since the word tetanus has long been used by pathologists to signify a diseased state, such as occurs in strychnine poisoning and hydrophobia, in which most of the muscles of the Body are thrown into prolonged and powerful involuntary contractions.

If, while a frog's muscle is still shortening under the influence of one electric shock, another stimulus be given it, it will contract again and the new contraction will be added on to that already existing, without any period of elongation occurring between them. While the muscle is still contract-

ing under the influence of the second stimulus a third electric shock will make it contract more, and so on, until the muscle is shortened as much as is possible to it for that strength of stimulus. If now the stimuli be repeated at the proper intervals, each new one will not produce any further shortening, but, each acting on the muscle before the effect of the last has begun to pass off, the muscle will be kept in a state of permanent or "tetanic" contraction; and this can be maintained, by continuing the application of the stimuli, until the organ begins to get exhausted or "fatigued"; elongation then commences in spite of the stimulation. When our muscles are stimulated in the Body, from the nerve-centres through the nerves, they receive from the latter a sufficient number of stimuli in a second (the exact number is still doubtful) to throw them into tetanic contractions. In other words, not even in the most rapid movements of the Body is a muscle made to execute a simple muscular contraction; it is always a longer or a shorter tetanus. When very quick movements are executed, as in performing rapid passages on the piano, the result is obtained by contracting two opposing muscles and alternately strengthening and weakening a little the tetanus of each.

Causes affecting the Degree of Muscular Contraction. The extent of shortening which can be called forth in a muscle varies with the stimulus. In the first place, a single stimulus can never cause a muscle to contract as much as rapidly repeated stimuli of the same strength—since in the latter case we get, as already explained, several simple contractions such as a single stimulus would call forth, piled on the top of one another. With powerful repeated electrical stimuli a muscle can be made to shorten to one third of its resting length, but in the Body the strongest effort of the Will never produces a contraction of that extent. Apart from the rate of stimulation, the strength of the stimulus has some influence, a greater stimulus causing a greater contraction; but very soon a point is reached beyond which increase of stimulus produces no increased contraction; the muscle has reached its limit. The amount of load carried by the muscle (or the resistance opposed to its shortening) has also an influence, and that in a very remarkable way. Suppose we have a frog's calf-muscle, carrying no weight, and find that with a stimulus of a certain strength it shortens two millimeters ($\frac{1}{13}$ inch).

Then if we hang one gram (15.5 grains) on it and give it the same stimulus, it will be found to contract more, say four or five millimeters, and so on, up to the point when it carries eight or ten grams. After that an increased weight will, with the same stimulus, cause a less contraction. So that up to a certain limit, resistance to the shortening of the muscle makes it more able to shorten: the mere greater extension of the muscle due to the greater resistance opposed to its shortening, puts it into a state in which it is able to contract more powerfully. Fatigue diminishes the working power of a muscle and rest restores it, especially if the circulation of the blood be going on in it at the same time. A frog's muscle cut out of the body will, however, be considerably restored during a period of rest, even although no blood flow through it.

Cold increases the time occupied by a simple muscular contraction, and also impairs the contractile power, as we find in our own limbs when " numbed " with cold, though in that case the hurtful influence of the cold on the nerves no doubt also plays a part. Moderate warmth on the other hand, up to near the point at which death stiffening (often in this case spoken of as *heat rigor*) occurs, diminishes the time taken by a contraction, and increases its height. Heat rigor is produced in excised frog's muscle by heating it to about 40° C. (104° F.) The required temperature is higher in warm blooded animals, especially while the circulation through the muscle is maintained: in fevers temperatures considerably greater than the above have been observed without the occurrence of muscular rigor.

The Measure of Muscular Work. The work done by a muscle in a given contraction, when it lifts a weight vertically against gravity, is measured by the weight moved, multiplied by the distance through which it is moved. When a muscle contracts carrying no load it does very little work, lifting only its own weight; when loaded with one gram and lifting it five millimeters it does five gram-millimeters of work, just as an engineer would say an engine had done so many kilogrammeters or foot-pounds. If loaded with ten grams and lifting it six millimeters it would do sixty gram-millimeters of work. Even after the weight becomes so great that it is lifted through a less distance, the work done by the muscle goes on increasing, for the heavier weight lifted more than compensates for the less distance through which it is

raised. For example, if the above muscle were loaded with fifty grams it would maybe lift that weight only 1.5 millimeters, but it would then do seventy-five gram-millimeters of work, which is more than when it lifted ten grams six millimeters. A load is, however, at last reached with which the muscle does less work, the lift becoming very little indeed, until at last the weight becomes so great that the muscle cannot lift it at all and so does no work when stimulated. Starting then from the time when the muscle carried no load and did no work, we pass with increasing weights, through phases in which it does more and more work, until with one particular load it does the greatest amount possible to it with that stimulus: after that, with increasing loads less work is done, until finally a load is reached with which the muscle again does no work. What is true of one muscle is of course true of all, and what is true of work done against gravity is true of all muscular work, so that there is one precise load with which a beast of burden or a man can do the greatest possible amount of work in a day. With a lighter or heavier load the distance through which it can be moved will be more or less, but the actual work done always less. In the living Body, however, the working of the muscles depends so much on other things, as the due action of the circulatory and respiratory systems and the nervous energy or "grit" (upon which the stimulation of the muscles depends) of the individual man or beast, that the greatest amount of work obtainable is not a simple mechanical problem as it is with the excised muscle.

From what precedes it is clear that the molecular changes which take place in a contracting muscle fibre are eminently susceptible of modification by slight changes in its environment. The evidence indicates that the contractility of a muscle depends, not upon a vital force entirely distinct from ordinary inanimate forces, but upon an arrangement of its material elements which is only maintained under certain conditions and is eminently modifiable by changes in the surroundings.

Influence of the Form of the Muscle on its Working Power. The amount of work that any muscle can do depends of course largely upon its physiological state; a healthy well-nourished muscle can do more than a diseased or starved one; but allowing for such variations the work which can be

done by a muscle varies with its form. The thicker the muscle, that is the greater the number of fibres present in a section made across the long axes of the fasciculi, the greater the load that can be lifted or the other resistance that can be overcome. On the other hand, the extent through which a muscle can move a weight increases with the length of its fasciculi. A muscle a foot in length can contract more than a muscle six inches long, and so would move a bone through a greater distance, provided the resistance were not too great for its strength. But if the shorter muscle had double the thickness, then it could lift twice the weight that the longer muscle could. We find in the Body muscles constructed on both plans; some to have a great range of movement, others to overcome great resistance, besides numerous intermediate forms which cannot be called either long and slender or short and thick; many short muscles for example are not specially thick, but are short merely because the parts on which they act lie near together. It must be borne in mind, too, that many apparently long muscles are really short stout ones— those namely in which a tendon runs down the side or middle of the muscle, and has the fibres inserted obliquely into it. The muscle (*gastrocnemius*) in the calf of the leg for instance (Fig. 53, *B*) is really a short stout muscle, for its working length depends on the length of its fasciculi and these are short and oblique, while its true cross-section is that at right angles to the fasciculi and is considerable. The force with which a muscle can shorten is very great. A frog's muscle of 1 square centimeter (0.39 inch) in section can just lift 2800 grams (98.5 ounces), and a human muscle of the same area more than twice as much.

Muscular Elasticity. A clear distinction must be made between elasticity and contractility. Elasticity is a physical property of matter in virtue of which various bodies tend to assume or retain a certain shape, and when removed from it, forcibly to return to it. When a spiral steel spring is stretched it will, if let go, "contract" in a certain sense, by virtue of its elasticity, but such a contraction is clearly quite different from a muscular contraction. The spring will only contract as a result of previous distortion; it cannot originate a change of form, while the muscle can actively contract or change its shape when a stimulus acts upon it, and that without being previously stretched. It does not merely tend to return to a

natural shape from which it has been removed, but it assumes a quite new natural shape, so that physiological contractility is a different thing from mere physical elasticity; the essential difference being that the coiled spring or a stretched band only gives back mechanical work which has already been spent on it, while the muscle originates work independently of any previous mechanical stretching. In addition to their contractility, however, muscles are highly elastic. If a fresh muscle be hung up and its length measured, and then a weight be hung upon it, it will stretch just like a piece of india-rubber, and when the weight is removed, provided it has not been so great as to injure the muscle, the latter will return passively, without any stimulus or active contraction, to its original form. In the Body all the muscles are so attached that they are usually a little stretched beyond their natural resting length; so that when a limb is amputated the muscles divided in the stump shrink away considerably. By this stretched state of the resting elastic muscles two things are gained. In the first place when the muscle contracts it is already taut, there is no "slack" to be hauled in before it pulls on the parts attached to its tendons: and, secondly, as we have already seen the working power of a muscle is increased by the presence of some resistance to its contraction, and this is always provided for from the first, by having the origin and insertion of the muscles so far apart as to be pulling on it when it begins to shorten.

The Electrical Currents of Muscle. When a muscle is exposed in the body or carefully removed from it and suitable electrodes connected with a sensitive galvanometer are applied to different parts of its surface, there is nearly always to be found evidence of a difference of electric potential between different parts of the muscle. These differences give rise to currents which are shown by the galvanometer to travel through the wires of the circuit from any central portion of the muscle to any part nearer one end, or from any part of the belly to a tendon. The less injured the muscle the more feeble are these currents, and in very fresh and very carefully exposed muscles they may be absent altogether. They are probably altogether absent from perfectly uninjured resting muscles, and when present in a resting muscle are due to the fact that any more living part of a muscle is electrically positive to a more injured or dead. When a muscle is exposed

its thinner ends die more quickly than its central parts, or the ends are directly injured when the muscle is cut across to remove it from the animal; and in that way the currents so usually observable arise. When all of a muscle is dead, its surface is isoelectric; no currents can be led off from it.

Even a quite uninjured muscle is however, capable, of giving rise to currents when it contracts, and these currents pass in such direction as to show that a portion of muscle in contraction is electronegative to a portion at rest. If a curarized muscle be stimulated at one point, its contraction commences at that point and travels from it over the remainder of the muscle; so that by the time a distant portion is in contraction the part which just contracted has come to rest. By electrodes suitably applied it can be observed that immediately after the stimulation the region of muscle close to the point of stimulation is electro-negative to a more distant part; but that afterwards, when a distant portion is in contraction and the stimulated region has returned to rest, the reverse is the case. Electrically, therefore, any contracting part of a muscle has to any resting part a relation similar to that of a dying or injured part of a muscle to an uninjured. The currents which arise in consequence of the changes going on in contracting muscle are known as the *action currents* to distinguish them from the *resting currents* due to unequal rates of death usually found between different parts of an exposed muscle in rest.

When a muscle is stimulated through its nerve the action current is less easy to demonstrate, because the nerve fibres branch all through the muscle and stimulate all parts of it at once, and throw all simultaneously into contraction. The current may, however, be shown indirectly. A muscle is removed with its nerve attached and electrodes put on it—one, for example, on the middle of the belly and the other on the tendon, so as to show on the galvanometer a resting current. If the muscle be now made to contract by stimulating its nerve the current is diminished, or, as is said, shows a *negative variation.* The cause of this is as follows: The amount of resting current depends on the difference between the less injured belly of the muscle and the injured end; anything which makes these two less different electrically must diminish this current; and as contracted muscle is electrically like dying muscle, when we throw the whole into activity the previously

existing difference is less than it was, and this the galva-
nometer shows as the negative variation.

Secondary Contraction. It is possible to use the action
current of one muscle to stimulate the nerve of a second and
produce a contraction. For this purpose two frogs' muscles,
A and *B*, are carefully dissected out with their nerves at-
tached. The nerve of *B* is laid over *A* so that one part of it
lies on the belly and another on the tendon. If the nerve
of *A* be stimulated by a single induction shock, for each
contraction of *A* we get a contraction of *B*, the negative
variation of the muscle current of *A* being the stimulus for
the nerve of *B*.

Secondary Tetanus. If the nerve of *A* be given rapidly
repeated stimuli so as to throw that muscle into tetanic con-
traction, *B* is also tetanized. This is of importance, as tend-
ing to show that the tetanus of *A* is really a compound con-
traction, although to the eye or as recorded by a lever it is one
unbroken shortening. If the electrical condition of *A*
remained uniform during contraction, there should be no
tetanus of *B*, but merely a simple contraction due to the set-
ting up of the action current or negative variation when *A*
commenced to contract, and a second due to the cessation of
this current when *A* came to rest again. The tetanus of *B*
must be due to rapidly repeated electrical variations in *A*, and
these probably correspond to the potentially separate con-
tractile changes going on in *A*, and fused into its apparently
uniform tetanic contraction.

The Source of Muscular Energy will be more fully dis-
cussed in the chapter on nutrition, but a few of the main
points may be mentioned here. A muscle where it contracts
is able to do work by using energy set free by chemical
changes occurring within it, as a steam-engine does work by
using the energy set free by the chemical changes occurring
in the combustion of its fuel; and as in the steam-engine,
so here, the fundamental change is an oxidative one, though in
the muscle a very indirect oxidation. A fresh frog's muscle
deprived of blood contains no uncombined oxygen; hung up
in an atmosphere of pure nitrogen it can be made to contract
and do a great deal of work before it dies and passes into
rigor mortis. While doing this work it gives off carbon-diox-
ide gas and becomes acid from the formation (probably) of
sarcolactic acid, but there does not appear to occur any ap-

preciable increase of oxygen-containing nitrogen compounds in it. As, under the conditions of the experiment, no free oxygen is available, the carbon dioxide must be derived from the breaking down of something present in the muscle; and as the formation of sarcolactic acid varies in amount with that of carbon dioxide, and both increase with the work done by the muscle, it would seem as if the energy set free were obtained by the breaking down of some highly unstable non-nitrogenous energy-yielding matter stored in the muscle. And such a view gains support from the fact that a man doing hard muscular work gives off per hour a great deal more carbon dioxide through his lungs than a man at rest, and does not give off any or very little more nitrogenous waste matter.

But a muscle placed as above described and made to work passes into rigor sooner than a muscle similarly situated and left at rest: and this shows that work tends to favor the production of myosin, or rather of its immediate precursor myosinogen, in the muscle: so here we get some evidence that the nitrogenous muscle constituents are influenced and altered though not oxidized during work. Further, when a muscle passes into rigor it gives off carbon-dioxide gas, whether it has been worked previously or not; if so situated as to be deprived of all exterior sources of supply, it gives off less when becoming rigid after work than when becoming rigid without having been worked; but the difference is almost accurately accounted for by the greater quantity of carbon dioxide the working muscle had previously given out. This suggests that the chemical phenomena of rigor and of work are essentially alike, being merely carried to an extreme in the former.

Most of the facts can be accounted for by the supposition that there is in living muscle a store of an unstable substance containing nitrogen, hydrogen, carbon, and oxygen. For this hypothetic substance the name *inogen* has been proposed. During work inogen is used up and broken into a highly oxidized part, carbon dioxide; an oxidized body containing carbon and hydrogen, as sarcolactic acid ($C_3H_6O_3$); and a third body allied to myosinogen and containing all the nitrogen and some of the oxygen, carbon, and hydrogen of the original inogen. In the products of this alteration stronger chemical affinities are satisfied than in the original compound,

and thus energy is liberated and used by the muscle. In the ordinary course of events the carbon dioxide is carried off by blood and lymph and eliminated from the Body; the sarco-lactic or other similar substance or substances are also carried off and oxidized elsewhere to form carbon dioxide and water and be then eliminated; but the nitrogen-containing product remains behind, and with the help of fresh oxygen and of other food material brought by the blood is reconstructed into, the original inogen. In the excised muscle there is but' scant store of material for repair; carbon dioxide is given off when the muscle contracts, and the sarcolactic acid and nitrogen-containing product accumulate: the latter then undergoes further changes, and ultimately becomes myosin. If the excised muscle be thrown into rigor quickly (as by heat), then the inogen is at once broken up, forming myosin and carbon dioxide and sarcolactic acid: if it be worked for a time before being thrown into rigor, then some of its inogen will have been already broken up, so there will be less to give rise to carbon dioxide at the moment of rigor, but the missing amount is found in that given off during work. If some such view as this, which may be called the "inogen theory," be the correct one, then the energy liberated by a resting muscle passing into rigor must take some other form than muscular work. As a matter of fact a good deal of heat is liberated during death stiffening, but whether sufficient to account for all the missing energy is by no means clear. The whole subject of the immediate source of muscular work is still in much need of elucidation.

Physiology of Plain Muscular Tissue. What has hither-to been said applies especially to the skeletal muscles; but in the main it is true of the unstriped muscles. These also are irritable and contractile, but their changes of form are much more slow than those of the striated fibres. Upon stimulation, a longer period of latent excitement elapses before the contraction commences and when, finally, this takes place it is comparatively very slow, gradually attaining a maximum and gradually passing away.

Unstriped muscular tissue has a remarkable power of remaining in the contracted state for long periods: the mus-cular coats of many small arteries, for example, are rarely relaxed; sometimes they may be more contracted, sometimes less, but in health seldom if ever completely at rest. There

seems to be some connection between that arrangement of the contractile substance which shows itself under the microscope as striation and the power of rapid contraction, since we find that the heart, which is not a skeletal or voluntary muscle but yet one that contracts rapidly, agrees with these in having its fibres striated. This connection is further illustrated by facts of comparative anatomy: insects are, as a rule, rapidly moving animals, and they are characterized by very marked striation of nearly all their muscular tissue; while in the slow-moving molluscs nearly all the muscular tissue is unstriped except in a few, as *Pecten*, which make rapid movements, and in that genus the muscles concerned in producing these movements are striated.

CHAPTER XI.

MOTION AND LOCOMOTION.

The Special Physiology of the Muscles. Having now considered separately the structure and properties in general of the skeleton, the joints, and the muscles, we may go on to consider how they all work together in the Body. Although the properties of muscular tissue are everywhere the same, the uses of different muscles are very varied, by reason of the different parts with which they are connected. Some are muscles of respiration, others of deglutition; many are known as *flexors* because they bend joints, others as *extensors* because they straighten them. The exact use of any particular muscle, acting alone or in concert with others, is known as its *special physiology*, as distinguished from its *general physiology*, or properties as a muscle without reference to its use as a muscle in a particular place. The functions of those muscles forming parts of the physiological mechanisms concerned in breathing and swallowing will be studied hereafter; for the present we may consider the muscles which co-operate in maintaining postures of the Body; in producing movements of its larger parts with reference to one another; and in producing *locomotion* or movement of the whole Body in space.

In nearly all cases the striped muscles carry out their functions with the co-operation of the skeleton, since nearly all are fixed to bones at each end, and when they contract primarily move these, and only secondarily the soft parts attached to them. To this general rule there are, however, exceptions. The muscle for example which lifts the upper eyelid and opens the eye arises from bone at the back of the orbit, but is inserted, not into bone, but into the eyelid directly; and similarly other muscles arising at the back of the orbit are directly fixed to the eyeball in front and serve to rotate it on the pad of fat on which it lies. Many facial muscles again have no direct attachment whatever to bones, as for example

the muscle (*orbicularis oris*) which surrounds the mouth-opening, and by its contraction narrows it and purses out the lips; or the *orbicularis palpebrarum* which similarly surrounds the eyes and when it contracts closes them.

Levers in the Body. When the muscles serve to move bones the latter are in nearly all cases to be regarded as levers whose fulcra lie at the joint where the movement takes place. Examples of all the three forms of levers recognized in mechanics are found in the Human Body.

Levers of the First Order. In this form (Fig. 63) the fulcrum or fixed point of support lies between the "weight"
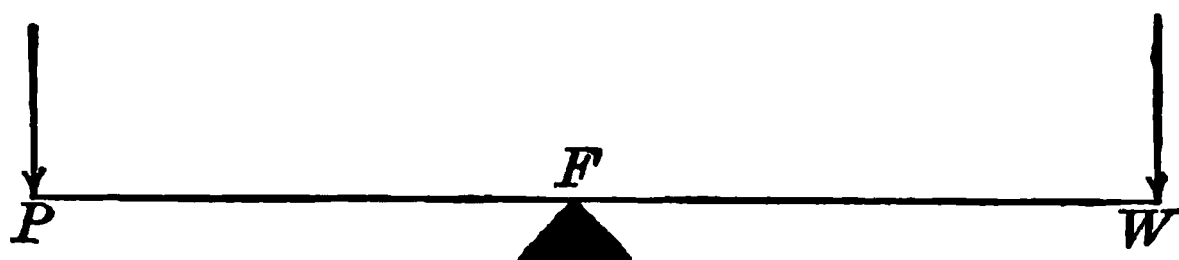
FIG. 63.—A lever of the first order. *F*, fulcrum; *P*, power; *W*, resistance or weight.

or resistance to be overcome and the "power" or moving force, as shown in the diagram. The distance *PF*, from the power to the fulcrum, is called the "power-arm;" the distance *FW* is the "weight-arm." When power-arm and weight-arm are equal, as is the case in the beam of an ordinary pair of scales, no mechanical advantage is gained, nor is there any loss or gain in the distance through which the weight is moved. For every inch through which *P* is depressed, *W* will be raised an equal distance. When the power-arm is longer than the other, then a smaller force at *P* will raise a larger weight at *W*, the gain being proportionate to the difference in the lengths of the arms. For example if *PF* is twice as long as *FW*, then half a kilogram applied at *P* will balance a whole kilogram at *W*, and just more than half a kilogram would lift it; but for every centimeter through which *P* descended, *W* would only be lifted half a centimeter. On the other hand when the weight-arm in a lever is longer than the power-arm, there is loss in force but a gain in the distance through which the weight is moved.

Examples of the first form of lever are not numerous in the Human Body. One is afforded in the nodding movements of the head, the fulcrum being the articulations between the skull and the atlas. When the chin is elevated the power is applied to the skull, behind the fulcrum, by

small muscles passing from the vertebral column to the occiput; the resistance is the excess in the weight of the part of the head in front of the fulcrum over that behind it, and is not great. To depress the chin as in nodding does not necessarily call for any muscular effort, as the head will fall forward of itself if the muscles keeping it erect cease to work, as those of us who have fallen asleep during a dull discourse on a hot day have learnt. If the chin however be depressed forcibly, as in the athletic feat of suspending one's self by the chin, the muscles passing from the chest to the skull in front of the atlanto-occipital articulation are called into play. Another example of the employment of the first form of lever in the Body is afforded by the curtsey with which a lady salutes another. In curtseying the trunk is bent forward at the hip-joints, which form the fulcrum; the weight is that of the trunk acting as if all concentrated at its centre of gravity, which lies a little above the sacrum and behind the hip-joints; and the power is afforded by muscles passing from the thighs to the front of the pelvis.

Levers of the Second Order. In this form the weight or resistance is between the power and the fulcrum. The power-arm PF is always longer than the weight-arm WF, and so a comparatively weak force can overcome a considerable resistance. But it is disadvantageous so far as regards rapidity and extent of movement, for it is obvious that when P is raised a certain distance W will be moved a less distance in the same time. As an example of the employment of such levers (Fig. 64) in the Body, we may take the act of standing on the toes. Here the foot represents the lever, the fulcrum is at the contact of its fore part with the ground ; the weight

Fig. 64.—A lever of the second order. *F.* fulcrum ; *P,* power ; *W,* weight. The arrows indicate the direction in which the forces act.

is that of the Body acting down through the ankle-joints at *Ta,* Fig. 65; and the power is the great muscle of the calf acting by its tendon inserted into the heel-bone (*Ca,* Fig. 65). Another example is afforded by holding up the thigh when one foot is kept raised from the ground, as in hopping on the

other.   Here the fulcrum is at the hip-joint, the power is applied at the knee-cap by a great muscle (*rectus femoris*) which

Fig. 65.—The skeleton of the foot from the outer side   *Th.* surface with which the leg-bones articulate ; *Ca.* the calcaneum into which the tendon (*tendo Achillis*) of the calf muscle is inserted ; *M5.* the metatarsal bone of the fifth digit ; *N,* the scaphoid bone ; *CI, CII, CIII,* first, second, and third cuneiform bones ; *Cb,* the cuboid bone.

is inserted there and arises from the pelvis; and the weight is that of the whole lower limb acting at its centre of gravity, which lies somewhere in the thigh between the hip and knee-joints, that is between the fulcrum and the point of application of the power.

Levers of the Third Order.   In these (Fig. 66) the power is between the fulcrum and the weight.   In such levers the weight-arm is always longer than the power-arm, so the power works at a mechanical disadvantage, but swiftness and range of movement are gained.   It is the lever most commonly used in the Human Body.   For example, when the forearm is bent up towards the arm, the fulcrum is the elbow-joint, the power is applied at the insertion of the biceps muscle (Fig. 52) into the radius and of another muscle (not represented in the figure, the *brachialis anticus,* into the ulna), and the
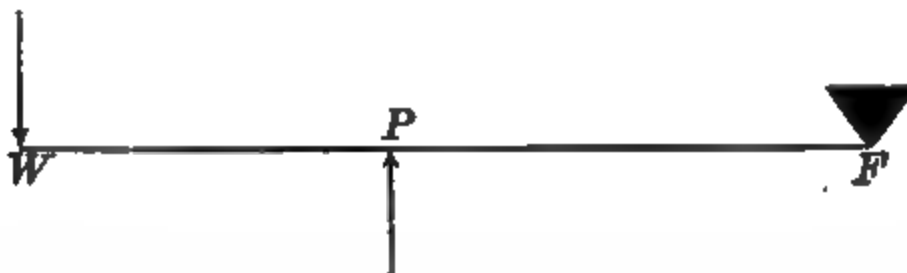
Fig. 66.—A lever of the third order.   *F,* fulcrum ; *P,* power ; *W,* weight.

weight is that of the forearm and hand, with whatever may be contained in the latter, acting at the centre of gravity of the whole somewhere on the distal side of the point of appli,

cation of the power. In the Body the power-arm is usually very short so as to gain speed and range of movement, the muscles being powerful enough to still do their work in spite of the mechanical disadvantage at which they are then placed. The limbs are thus made much more shapely than would be the case were the power applied near or beyond the weight.

It is of course only rarely that simple movements as those described above take place. In the great majority of those executed several or many muscles co-operate.

The Loss to the Muscles from the Direction of their Pull. It is worthy of note that, owing to the oblique direction in which the muscles are commonly inserted into the bones, much of their force is lost so far as producing movement is concerned. Suppose the log of wood in the diagram (Fig. 67) to be raised by pulling on the rope in the direction *a*; it is clear at first that the rope will act at a great disadvantage; most of the pull transmitted by it will be exerted against the pivot on which the log hinges, and only a small fraction be available for elevating the latter. But the more the log is lifted, as for example into the position indicated by the dotted lines, the more useful will be the direction of the pull, and the more of it will be spent on the log and the less lost unavailingly in merely increasing the pressure at the hinge. If we now consider the action of the biceps (Fig. 52) in flexing the elbow-joint, we see similarly that the straighter the joint is, the more of the pull of the muscle is wasted. Beginning
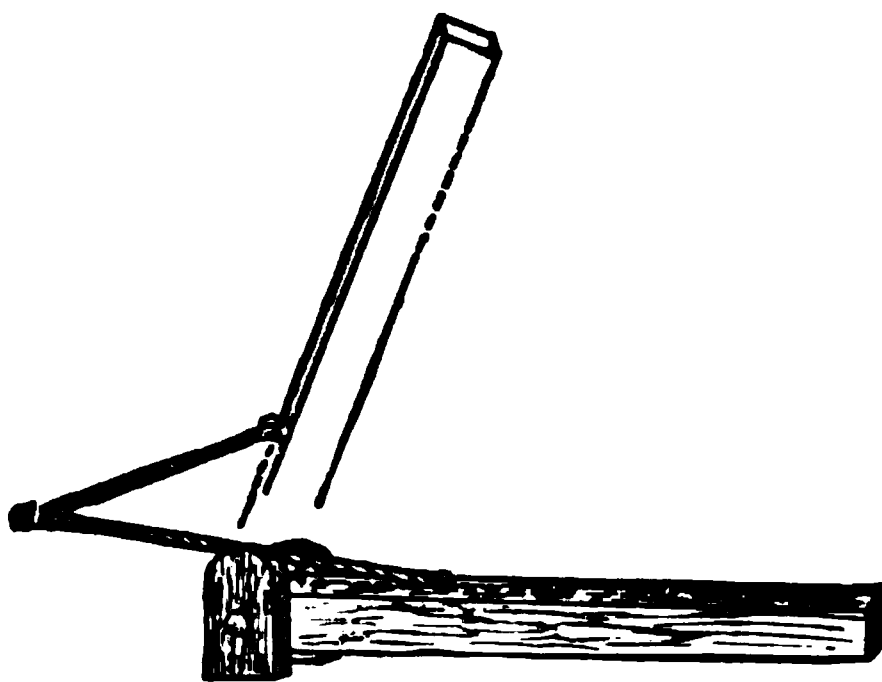
Fig. 67.—Diagram illustrating the disadvantage of an oblique pull.

with the arm straight, it works at a great disadvantage, but as the forearm is raised the conditions become more and more

favorable to the muscle. Those who have practised the gymnastic feat of raising one's self by bending the elbows when hanging by the hands from a horizontal bar know practically that if the elbow-joints are quite straight it is very hard to start; and that, on the other hand, if they are kept a little flexed at the beginning the effort needed is much less; the reason being of course the more advantageous direction of traction by the biceps in the latter case.

Experiment proves that the power with which a muscle can contract is greatest at the commencement of its shortening, the very time at which, we have just seen, it works at most mechanical disadvantage; in proportion as its force becomes less the conditions become more favorable to it. There is, however, it is clear, nearly always a considerable loss of power in the working of the skeletal muscles, strength being sacrificed for variety, ease, rapidity, extent, and elegance of movement.

Postures. The term posture is applied to those positions of equilibrium of the Body which can be maintained for some time, such as standing, sitting, or lying, compared with leaping, running, or falling. In all postures the condition of stability is that the vertical line drawn through the centre of gravity of the body shall fall within the basis of support afforded by objects with which it is in contact ; and the security of the posture is proportionate to the extent of this base, for the wider it is the less is the risk of the perpendicular through the centre of gravity falling outside of it on slight displacement.

The Erect Posture. This is pre-eminently characteristic of man, his whole skeleton being modified with reference to it. Nevertheless the power of maintaining it is only slowly learnt in the first years after birth, and for a long while it is unsafe. And though finally we learn to stand erect without conscious attention, the maintenance of that posture always requires the co-operation of many muscles, co-ordinated by the nervous system. The influence of the latter is shown by the fall which follows a severe blow on the head, which may nevertheless have fractured no bone nor injured any muscle : the concussion of the brain, as we say, "stuns" the man, and until its effects have passed off he cannot stand upright. In standing with the arms straight by the sides and the feet together the centre of gravity of the whole adult Body lies

in the articulation between the sacrum and the last lumbar vertebra, and the perpendicular drawn from it will reach the ground between the two feet, within the basis of support afforded by them. With the feet close together, however, the posture is not very stable, and in standing we commonly make it more so by slightly separating them so as to increase the base. The more one foot is in front of the other the more swaying back and forward will be compatible with safety; and the greater the lateral distance separating them the greater will be the lateral sway which is possible without falling. Consequently we see that a man about to make great movements with the upper part of his Body, as in fencing or boxing, or a soldier preparing for the bayonet exercise, always commences by thrusting one foot forwards obliquely, so as to increase his basis of support in both directions.

The ease with which we can stand is largely dependent upon the way in which the head is almost balanced on the top of the vertebral column, so that but little muscular effort is needed to keep it upright. In the same way the trunk is almost balanced on the hip joints, but not quite, its centre of gravity falling rather behind them; so that just as some muscular effort is needed to keep the head from falling forwards, some is needed to keep the trunk from toppling backwards at the hips. In a similar manner other muscles are called into play at other joints: as between the vertebral column and the pelvis, and at the knees and ankles; and thus a certain rigidity, due to muscular effort, extends all along the erect Body: which, on account of the flexibility of its joints, could not otherwise be balanced on its feet, as a statue can. Beginning (Fig. 68) at the ankle-joint, we find it kept stiff in standing by the combined and balanced contraction of the muscles passing from the heel to the thigh, and from the dorsum of the foot to the shin-bone (*tibia*).

Fig. 68.—Diagram illustrating the muscles (drawn in thick black lines) which pass before and behind the joints and by their balanced activity keep the joints rigid and the body erect.

Others passing before and behind the knee-joint keep it from yielding; and so at the hip-joints: and others again, lying in the walls of the abdomen and along the vertebral column, keep the latter rigid and erect on the pelvis; and finally the skull is kept in position by muscles passing from the sternum and vertebral column to it, in front of and behind the occipital condyles.

Locomotion includes all the motions of the whole Body in space, dependent on its own muscular efforts: such as walking, running, leaping, and swimming.

Walking. In walking the Body never entirely quits the ground, the heel of the advanced foot touching the ground in each step before the toe of the rear foot leaves it. The advanced limb supports the Body, and the foot in the rear at the commencement of each step propels it.

Suppose a man standing with his heels together to commence to walk, stepping out with the left foot; the whole Body is at first inclined forwards, the movement taking place mainly at the ankle-joints. By this means the centre of gravity would be thrown in front of the base formed by the feet and a fall on the face result, were not simultaneously the left foot slightly raised by bending the knee and then swung forwards, the toes just clear of the ground and, in good walking, the sole nearly parallel to it. When the step is completed the left knee is straightened and the sole placed on the ground, the heel touching it first, and the base of support being thus widened from before back, a fall is prevented. Meanwhile the right leg is kept straight, but inclines forwards above with the trunk when the latter advances, and as this occurs the sole gradually leaves the ground, commencing with the heel. When the step of the left leg is completed the great toe of the right alone is in contact with the support. With this a push is given which sends the trunk on over the left leg, which is now kept rigid, except at the ankle-joint; and the right knee being bent that limb swings forwards, its foot just clearing the ground as the left did before. The Body is meanwhile supported on the left foot alone, but when the right completes its step the knee of that leg is straightened and the foot thus placed, heel first, on the ground. Meanwhile the left foot has been gradually leaving the ground, and its toes only are at that moment upon it: from these a push is given, as before, with the right foot, and the

knee being bent so as to raise the foot, the left leg swings forwards at the hip-joint to make a fresh step.

During each step the whole Body sways up and down and also from side to side. It is highest at the moment when the advancing trunk is vertically over the foot supporting it, and then sinks until the moment when the advancing foot touches the ground, when it is lowest. From this moment it rises as it swings forward on this foot, until it is vertically over it, and then sinks again until the other touches the ground; and so on. At the same time, as its weight is alternately transferred from the right to the left foot and *vice versa,* there is a slight lateral sway, commonly more marked in women than in men, and which when excessive produces an ugly "waddling" gait.

The length of each step is primarily dependent on the length of the legs; but can be controlled within wide limits by special muscular effort. In easy walking little muscular work is employed to carry the rear leg forwards after it has given its push. When its foot is raised from the ground it swings on, like a pendulum; but in fast walking the muscles, passing in front of the hip-joint, from the pelvis to the limb, by their contraction forcibly carry the leg forwards. The easiest step, that in which there is most economy of labor, is that in which the limb is let swing freely, and since a short pendulum swings faster than a longer, the natural step of short-legged people is quicker than that of long-legged ones.

In fast walking the advanced or supporting leg also aids in propulsion; the muscles passing in front of the ankle-joint contracting so as to pull the Body forwards over that foot and aid the push from the rear foot. Hence the fatigue and pain in front of the shin which is felt in prolonged, very fast walking. From the fact that each foot reaches the ground heel first, but leaves it toe last, the length of each stride is increased by the length of the foot.

Running. In this mode of progression there is a moment in each step when both feet are off the ground, the Body being unsupported in the air. The toes alone come in contact with the ground at each step, and the knee-joint is not straight when the foot reaches the ground. When the rear foot is to leave the support, the knee is suddenly straightened, and at the same time the ankle-joint is extended so as

to push the toes forcibly on the ground and give the whole Body a powerful push forwards and upwards. Immediately after this the knee is greatly flexed and the foot raised from the ground, and this occurs before the toes of the forward foot reach the latter. The swinging leg in each step is violently pulled forwards and not suffered to swing naturally, as in walking. By this the rapidity of the succession of steps is increased, and at the same time the stride is made greater by the sort of one-legged leap that occurs through the jerk given by the straightening of the knee of the rear leg just before it leaves the ground.

Leaping. In this mode of progression the Body is raised completely from the ground for a considerable period. In a powerful leap the ankles, knees, and hip-joints are all flexed as a preparatory measure, so that the Body assumes a crouching attitude. The heels, next, are raised from the ground and the Body balanced on the toes. The centre of gravity of the Body is then thrown forwards, and simultaneously the flexed joints are straightened, and by the resistance of the ground, the Body receives a propulsion forwards; much in the same way as a ball rebounds from a wall. The arms are at the same time thrown forwards. In leaping backwards, the Body and arms are inclined in that direction; and in jumping vertically there is no leaning either way and the arms are kept by the sides.

Hygiene of the Muscles. The healthy working of the muscles needs of course a healthy state of the Body generally, so that they shall be supplied with proper materials for growth and repair, and have their wastes rapidly and efficiently removed. In other words, good food and pure air are necessary for a vigorous muscular system, a fact which trainers recognize in insisting upon a strict dietary, and in supervising generally the mode of life of those who are to engage in athletic contests. The muscles should also not be exposed to any considerable continued pressure, since this interferes with the flow of blood and lymph through them.

As far as the muscles themselves are directly concerned, exercise is the necessary condition of their best development. A muscle which is permanently unused degenerates and is absorbed, little finally being left but the connective tissue of the organ and a few muscle fibres filled with oil-drops. This is well seen in cases of paralysis dependent on injury to the

nerves. In such cases the muscles may themselves be per-
fectly healthy at first, but lying unused for weeks they become
altered, and finally, when the nervous injury has been healed,
the muscles may be found. incapable of functional activity.
The physician therefore is often careful to avoid this by exer-
cising the paralyzed muscles daily by means of electrical
shocks sent through the part, while at the same time he tries
to restore the nerves; passive exercise, as by proper massage,
is frequently of great use in such cases. The same fact is
illustrated by the feeble and wasted condition of the muscles
of a limb which has been kept for some time in splints. After
the latter have been removed it is only slowly, by judicious
and persistent exercise, that the long-idle muscles regain
their former size and power. The great muscles of the
"brawny" arm of the blacksmith or wrestler illustrate the
reverse fact, the growth of the muscles by exercise. Exer-
cise, however, must be judicious; repeated frequently to the
point of exhaustion it does harm; the period of repair is not
sufficient to allow replacement of the parts used in work, and
the muscles thus waste under too violent exercise as with too
little. Rest should alternate with work, and that regularly,
if benefit is to be obtained. Moreover, violent exercise should
never be suddenly undertaken by one unused to it, not
only lest the muscles suffer, but because muscular effort
greatly increases the work of the heart, not merely because
more blood has to be sent to the muscles themselves, but they
produce great quantities of carbon dioxide, which must be
carried off in the blood to the lungs for removal from the
Body, and the heart must work harder to send the blood faster
through the lungs, and at the same time the breathing be
hastened so as to renew the air in those organs faster. The
least evil result of throwing too violent work on the heart
and lungs in this way is represented by being "out of
breath," which is advantageous insomuch as it may lead to a
cessation of the exertion. But much more serious, and
sometimes permanent, injuries of either the circulatory or
respiratory organs may be caused by violent and prolonged
efforts without due previous training. No general rule can
be laid down as to the amount of exercise to be taken; for a
healthy man in business the minimum would perhaps be rep-
resented by a daily walk of five miles.

Varieties of Exercise. In walking and running the

muscles chiefly employed are those of the lower limbs and trunk. This is in part true of rowing, which when good is performed much more by the legs than the arms: especially since the introduction of sliding seats. Hence any of these exercises alone is apt to leave the muscles of the chest and arms imperfectly exercised. Indeed, no one exercise employs equally or proportionately all the muscles: therefore gymnasia in which various feats of agility are practised, so as to call different parts into play, have very great utility. It should be borne in mind, however, that the legs especially need strength; while the upper limbs, in which delicacy of movement, as a rule, is more desirable than power, do not require so much exercise; and the fact that gymnastic exercises are commonly carried on indoors is a great drawback to their value. When the weather permits, out-of-door exercise is far better than that carried on in even the best ventilated and lighted gymnasium. For those who are so fortunate as to possess a garden there is no better exercise, at suitable seasons, than an hour's daily digging in it; since this calls into play nearly all the muscles of the Body; while of games, the modern one of lawn tennis is perhaps the best from a hygienic view that has ever been invented, since it not only demands great muscular agility in every part of tne Body, but trains the hand to work with the eye in a way that walking, running, rowing, and similar pursuits do not. For the same reasons baseball, cricket, and boxing are excellent.

Exercise in Infancy and Childhood. Young children have not only to strengthen their muscles by exercise, but also to learn to use them. Watch an infant trying to convey something to its mouth, and you will see how little control it has over its muscles. On the other hand, the healthy infant is never at rest when awake; it constantly throws its limbs around, grasps at all objects within its reach, coils itself about, and so gradually learns to exercise its powers. It is a good plan to leave every healthy child more than a few months old several times daily on a large bed, or even on a rug or carpeted floor, with as little covering as is safe, and that as loose as possible, and let it wriggle about as it pleases. In this way it will not only enjoy itself thoroughly, but gain strength and a knowledge of how to use its limbs. To keep a healthy child swathed all day in tight and heavy clothes is cruelty.

When a little later the infant commences to crawl it is safe to permit it to as much as it wishes, but unwise to tempt it to do so when disinclined: the bones and muscles are still feeble and may be injured by too much work. The same is true of learning to walk.

From four or five to twelve years of age almost any form of exercise should be permitted, or even encouraged. During this time, however, the epiphyses of many bones are not firmly united to their shafts, and so anything tending to throw too great a strain on the joints should be avoided. After that up to commencing manhood or maidenhood any kind of out-door exercise for healthy persons is good, and girls are all the better for being allowed to join in their brothers' sports. Half of the debility and general ill-health of so many of our women is the consequence of deficient exercise during early life; and the day, which fortunately seems approaching, which will see dolls as unknown to or as despised by healthy girls as by healthy boys will see the beginning of a great improvement in the stamina of the female portion of our popu-lation.

Exercise in Youth should be regulated largely by sex; not that women are to be shut up and made pale, delicate, and unfit to share the duties or participate fully in the pleasures of life; but the other calls on the strength of the young woman render vigorous muscular work often unadvisable, especially under conditions where it is apt to be followed by a chill.

A healthy boy or young man may do nearly anything; but until twenty-two or twenty-three very prolonged effort is un-advisable. The frame is still not firmly knit or as capable of endurance as it will subsequently become.

Girls should be allowed to ride or play out-door games in moderation, and in any case should not be cribbed in tight stays or tight boots. A flannel dress and proper lawn tennis shoes are as necessary for the healthy and safe enjoyment of an afternoon at that game by a girl as they are for her brother in the baseball field. Rowing is excellent for girls if there be any one to teach them to do it properly with the legs and back, and not with the arms only, as women are so apt to row. Properly practised it strengthens the back and improves the carriage.

Exercise in Adult Life. Up to forty a man may carry on safely the exercises of youth, but after that sudden efforts

should be avoided. A lad of twenty-one or so may, if trained, safely run a quarter-mile race, but to a man of forty-five it would be dangerous, for with the rigidity of the cartilages and blood-vessels which begins to show itself about that time comes a diminished power of meeting a sudden violent demand. On the other hand, the man of thirty would more safely than the lad of nineteen or twenty undertake one of the long-distance walking matches which have lately been in vogue; the prolonged effort would be less dangerous to him, though a six-days' match, with its attendant loss of sleep, cannot fail to be more or less dangerous to any one. Probably for one engaged in active business a walk of two or three miles to it in the morning and back again in the afternoon is the best and most available exercise. The habit which Americans have everywhere acquired, of never walking when they can take a street car, is certainly detrimental to the general health; though the extremes of heat and cold to which we are subject often render it unavoidable.

For women during middle life the same rules apply: there should be some regular but not violent daily exercise.

In Old Age the needful amount of exercise is less, and it is still more important to avoid sudden or violent effort.

Exercise for Invalids. This should be regulated under medical advice. For feeble persons gymnastic exercises are especially valuable, since from their variety they permit of selection according to the condition of the individual; and their amount can be conveniently controlled.

Training. If any person attempt some unusual exercise he soon finds that he loses breath, gets perhaps a "stitch in the side," and feels his heart beating with unwonted violence. If he persevere he will probably faint—or vomit, as is frequently seen in the case of imperfectly trained men at the end of a hard boat-race. These phenomena are avoided by careful gradual preparation known as "training." The immediate cause of them lies in disturbances of the circulatory and respiratory organs, on which excessive work is thrown.

CHAPTER XII.

ANATOMY OF THE NERVOUS SYSTEM.

Nerve-Trunks. In dissecting the Human Body numerous white cords are found which at first sight might be taken for tendons. That they are something else however soon becomes clear, since a great many of them have no connection with muscles at all, and those which have usually enter somewhere into the belly of the muscle, instead of being fixed to its ends as most tendons are. These cords are *nerve-trunks*: followed in one direction each (Fig. 69) will be found to break up into finer and finer branches, until the subdivisions become too small to be followed without the aid of a microscope. Traced the other way the trunk will in most cases be found to increase by the union of others with it, and ultimately to join a much larger mass of different structure, from which other trunks also spring. This mass is a *nerve-centre.* That end of a nerve attached to the centre is naturally its *central,* and the other its *distal* or *peripheral end.* Nerve-centres, then, give origin to nerve-trunks; these latter spread all over the Body, usually branching and becoming smaller and smaller as they proceed from the centre; they finally become very small, and how they ultimately end is not in all cases certain, but it is known that some have sense-organs at their terminations and others muscular fibres. The general arrangement of the larger nerve-trunks of the Body is shown in Fig. 69. Physically a nerve is not so tough or strong as a tendon of the same size; it may readily be split up into longitudinal strands, each of which consists of a number of microscopic threads, the *nerve-fibres,* bound together by connective tissue.

Plexuses. Very frequently several neighboring nerve-trunks send off communicating branches to one another, each branch carrying fibres from one trunk to the other. Such networks are called *plexuses* (Fig. 72), and through the interchanges taking place in them it often happens that the distal

branches of a nerve-trunk contain fibres which it does not possess as it leaves the centre to which it is connected.

FIG. 68.—Diagram illustrating the general arrangement of the nervous system.

Nerve-Centres. The great majority of the nerves take their origin from the *brain* and *spinal cord*, which together form the great *cerebro-spinal centre.* Some, however, com-

mence in rounded or oval masses which vary in size from that of the kernel of an almond down to microscopic dimensions, and which are widely distributed in the Body. Each of these smaller scattered centres is called a *ganglion,* and the whole of them are arranged in three sets. A considerable number of the largest are united directly to one another by nerve-trunks, and also give off nerves to various organs, especially to the blood-vessels and the viscera in the thoracic and abdominal cavities. These ganglia and their branches form the *sympathetic nervous system,* as distinguished from the cerebro-spinal nervous system consisting of the brain and spinal cord and the nerves springing from them. Of the remaining ganglia some are connected with various cerebrospinal trunks near their origin, while the rest, for the most part very small and connected with the peripheral branches of sympathetic or other nerves, are known as the *sporadic ganglia.*

The Cerebro-Spinal Centre and its Membranes. Lying inside the skull is the *brain* and in the neural canal of the vertebral column the *spinal cord* or *spinal marrow,* the two being continuous through the *foramen magnum* of the occipital bone and forming the great cerebro-spinal nerve-centre. This centre is bilaterally symmetrical throughout except for slight differences on the surfaces of parts of the brain, which are often found in the higher races of mankind. Both brain and spinal cord are very soft and easily crushed, the connective tissue and a peculiar supporting tissue (*neuroglia*) which pervade them being delicate; accordingly both organs are placed in nearly completely closed bony cavities and are also enveloped by membranes which give them support. These membranes are three in number. Externally is the *dura mater,* very tough and strong and composed of white fibrous and elastic connective tissues. In the cranium the dura mater adheres by its outer surface to the inside of the skull chamber, serving as the periosteum of its bones; this is not the case in the vertebral column, where the dura mater forms a loose sheath around the spinal cord and is only attached here and there to the surrounding bones, which have a separate periosteum of their own. The innermost membrane of the cerebro-spinal centre, lying in immediate contact with the proper nervous parts, is the *pia mater,* also made up of white fibrous tissue interwoven with elastic fibres, but less

closely than in the dura mater, so as to form a less dense and
tough membrane. The pia mater
contains many blood-vessels which
break up in it into small branches
before entering the nervous mass
beneath. Covering the outside of
the pia mater is a layer of flat closely
fitting cells; a similar layer lines the
inside of the dura mater, and these
two layers are described as the third
membrane of the cerebro-spinal cen-
tre, called the *arachnoid*. In the
space between the two layers of the
arachnoid is contained a small quan-
tity of watery *cerebro-spinal liquid*.
The surface of the brain is folded
and the pia mater follows closely these
folds; the arachnoid often stretches
across them: in the spaces thus left
between it and the pia mater is con-
tained some of the cerebro-spinal
liquid.

The **Spinal Cord** (Fig. 70) is
nearly cylindrical in form, being
however a little wider from side to
side than dorsoventrally, and taper-
ing off at its posterior end. Its
average diameter is about 19 milli-
meters ($\frac{3}{4}$ inch) and its length 0.43
meter (17 inches). It weighs 42.5
grams ($1\frac{1}{2}$ ounces). There is no
marked limit between the spinal cord
and the brain, the one passing grad-
ually into the other (Fig. 77), but
the cord is arbitrarily said to com-
mence opposite the outer margin of
the foramen magnum of the occipital
bone: from there it extends to the
articulation between the first and
second lumbar vertebræ, where it
narrows off to a slender filament, the
filum terminale (cut off and represented separately at *B* in Fig.

FIG. 70.—The spinal cord and
medulla oblongata. A. from the
ventral, and *B.* from the dorsal
aspect; *C* to *H* cross-sections at
different levels.

70), which runs back to the end of the neural canal behind the sacrum. In its course the cord presents two expansions, an upper, 10, the *cervical enlargement*, reaching from the third cervical to the first dorsal vertebræ, and a lower or *lumbar enlargement*, 9, opposite the last dorsal vertebra.

Running along the middle line on both the ventral and the dorsal aspects of the cord is a groove, and a cross-section shows that these grooves are the surface indications of fissures which extend deeply into the cord (*C*, Fig. 71) and nearly divide it into right and left halves.

The *anterior fissure* (1, Fig. 71) is wider and shallower than the *posterior*, 2, which indeed is hardly a true fissure, being completely filled up by an ingrowth of pia mater. The transverse section, *C*, shows also that the substance of the

Fig. 71.—The spinal cord and nerve-roots. *A*, a small portion of the cord seen from the ventral side; *B* the same seen laterally; *C*, a cross section of the cord; *D*, the two roots of a spinal nerve; 1 anterior (ventral) fissure; 2, posterior (dorsal) fissure; 3, surface groove along the line of attachment of the anterior nerve-roots; 4, line of origin of the posterior roots; 5, anterior root filaments of spinal nerve; 6, posterior root filaments; 6′, ganglion of the posterior root; 7, 7′, the first two divisions of the nerve-trunk after its formation by the union of the two roots. The grooves are much exaggerated

cord is not alike throughout, but that its *white* superficial layers envelop a central *gray substance* arranged somewhat in the form of a capital H. Each half of the gray matter is crescent-shaped, and the crescents are turned back to back and united across the middle line by the *gray commissure*. The

tips of each crescent are called its horns or *cornua*, and the ventral, or *anterior cornu*, on each side is thicker and larger than the posterior. In the cervical and lumbar enlargements the proportion of white to gray matter is greater than elsewhere; and as the cord approaches the medulla oblongata its central gray mass becomes irregular in form and begins to break up into smaller portions. If lines be drawn on the transverse section of the cord from the tip of each horn of the gray matter to the nearest point of the surface, the white substance in each half will be divided into three portions: one between the anterior fissure and the anterior cornu, and called the *anterior white column ;* one between the posterior fissure and the posterior cornu, and called the *posterior white column ;* while the remaining one lying in the hollow of the crescent and between the two horns is the *lateral column :* the anterior and lateral columns of the same side are frequently named the *antero-lateral column.* A certain amount of white substance crosses the middle line at the bottom of the anterior fissure; this forms the *anterior white commissure.* There is no posterior white commissure, the bottom of the posterior fissure being the only portion of the cord where the gray substance is uncovered by white. Running along the middle of the gray commissure, for the whole length of the cord, is a tiny channel, just visible to the unaided eye; it is known as the *central canal* (*canalis centralis*).

The Spinal Nerves. Thirty-one pairs of spinal nerve-trunks enter the neural canal of the vertebral column through the intervertebral foramina (p. 71). Each divides in the foramen into a dorsal and ventral portion known respectively as the *posterior* and *anterior roots* of the nerve (6 and 5, Fig. 71), and these again subdivide into finer branches which are attached to the sides of the cord, the posterior root at the point where the posterior and lateral white columns meet, and the anterior root at the junction of the lateral and anterior columns. At the lines on which the roots are attached there are superficial furrows on the surface of the cord. On each posterior root is a *spinal ganglion* (6′, Fig. 71), placed just before it joins the anterior root to make up the common nerve-trunk. Immediately after its formation by the mixture of fibres from both roots, the trunk divides (*D*, Fig. 71), into a *posterior primary*, an *anterior primary*, and a *communicating branch.* The branches of the first set go for the most

part to the skin and muscles on the back, the second form a series of plexuses from which the nerves for the sides and ventral region of the neck and trunk and for the limbs arise; the communicating branches go to neighboring sympathetic ganglia.

The various spinal nerves are named from the portions of the vertebral column through the intervertebral foramina of which they pass out; and as a general rule each nerve is named from the vertebra in front of it. For example the nerve passing out between the fifth and sixth thoracic vertebræ is the "fifth thoracic" nerve, and that between the last thoracic and first lumbar vertebræ, the "twelfth thoracic." In the cervical region, however, this rule is not adhered to. The nerve passing out between the occipital bone and the atlas is called the "first cervical" nerve, that between the atlas and axis the second, and so on; that between seventh cervical and first thoracic vertebræ being the "eighth cervical" nerve. The thirty-one pairs of spinal nerves are then thus distributed: 8 cervical, 12 thoracic, 5 lumbar, 5 sacral, and 1 coccygeal; the latter passing out between the sacrum and coccyx. Since the spinal cord ends opposite the upper lumbar vertebræ while the sacral and coccygeal nerves pass out from the neural canal much farther back, it is clear that the roots of those nerves, on their way to unite in the foramina of exit and form nerve-trunks, must run obliquely backwards in the spinal canal for a considerable distance. One finds in fact the neural canal in the lumbar and sacral regions, behind the point where the spinal cord has tapered off to form the *filum terminale*, occupied chiefly by a great bunch of nerve-roots forming the so-called "horse's tail" or *cauda equina*.

Distribution of the Spinal Nerves. It would be out of place here to go into detail as to the exact portions of the Body supplied by each spinal nerve, but the following general statements may be made. The anterior primary branches of the first four cervical nerves form on each side the *cervical plexus* (Fig. 72) from which branches are supplied to the muscles and integument of the neck: also to the outer ear and the back part of the scalp. The anterior primary branches of the remaining cervical nerves and the first dorsal form the *brachial plexus*, from which the upper limb is supplied. The roots of the trunks which form this plexus arise from the cervical enlargement of the spinal cord.

From the fourth and fifth cervical nerves on each side, small branches arise and unite to make the *phrenic nerve* (4', Fig. 72) which runs down through the chest and ends in the diaphragm.

The anterior primary branches of the dorsal nerves, except part of the first which enters the brachial plexus, form no

C

Fig. 72.—The cervical and brachial plexuses of the left side of the Body.

plexus, but each runs along the posterior border of a rib and supplies branches to the chest-walls, and the lower ones to those of the abdomen also.

The anterior primary branches of the four anterior lumbar nerves are united by branches to form the *lumbar plexus.*

It supplies the lower part of the trunk, the buttocks, the front of the thigh, and inner side of the leg.

The *sacral plexus* is formed by the anterior primary branches of the fifth lumbar and the first four sacral nerves, which unite in one great cord and so form the *sciatic nerve*, which is the largest in the Body and, running down the back of the thigh, ends in branches for the lower limb. The roots of the trunks which form the sacral plexus arise from the lumber enlargement of the cord.

The Brain (Fig. 73) is far larger than the spinal cord and more complex in structure. It weighs on the average
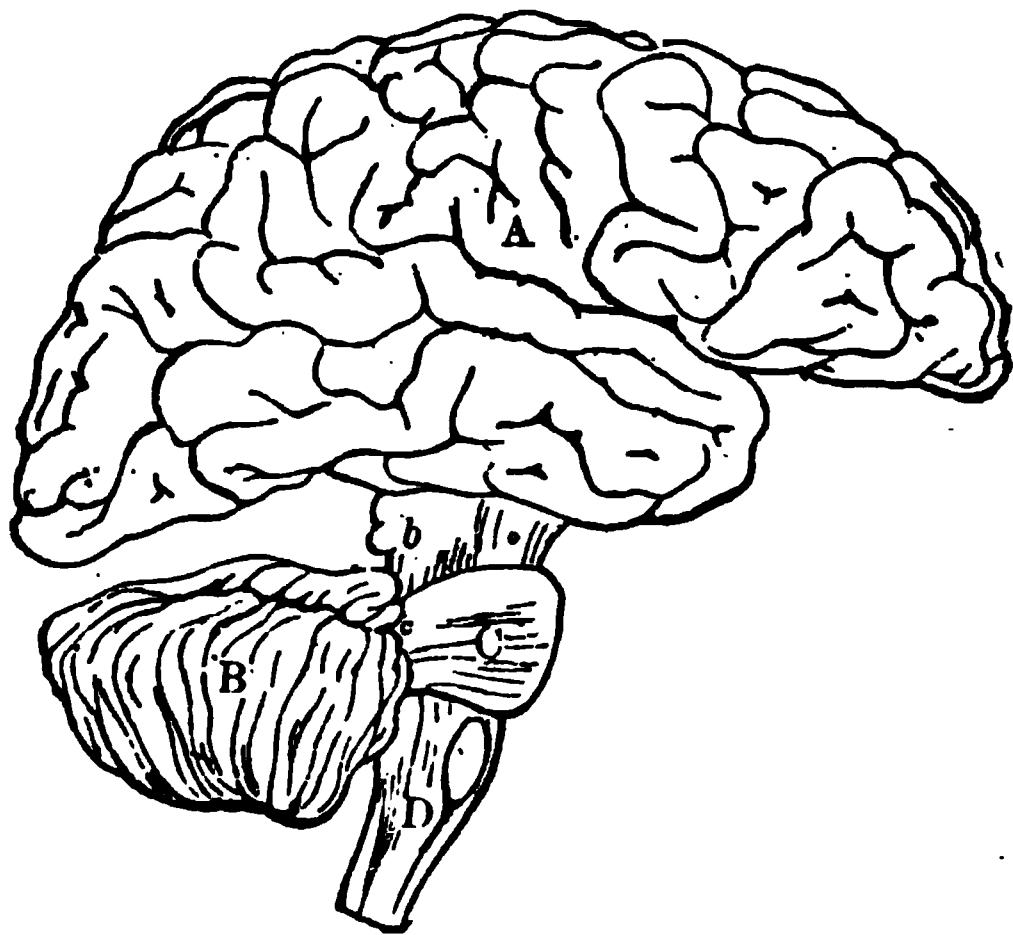
Fig 73.—Diagram illustrating the general relationships of the parts of the brain. *A*, fore-brain; *b*. mid-brain ; *B*. cerebellum; *C*. pons Varolii ; *D*. medulla oblongata ; *B*, *C*, and *D* together constitute the hind-brain.

about 1415 grams (50 ounces) in the adult male, and about 155 grams (5.5 ounces) less in the female. In its simpler forms the vertebrate brain consists of three masses, each with subsidiary parts, following one another in series from before back, and known as the fore-brain, mid-brain, and hind-brain respectively. In man the fore-brain, *A*, weighing about 1245 grams (44 ounces), is much larger than all the rest put together and laps over them behind. It consists mainly of two large convoluted masses, separated from one another by a deep median fissure, and known as the *cerebral hemispheres*. The immense proportionate size of these is very characteristic of the human brain. Beneath each cere-

bral hemisphere is an *olfactory lobe,* inconspicuous in man but in many animals larger than the cerebral hemispheres. Buried in the fore-brain on each side are two large gray masses, the *corpora striata* and *optic thalami.* The mid-brain forms a connecting isthmus between the two other divisions and presents on its dorsal side four hemispherical eminences, the *corpora quadrigemina.* On its ventral side it exhibits two semicylindrical pillars (seen under the nerve *IV.* in Fig. 77), known as the *crura cerebri.* The hind-brain consists of three main parts : on its dorsal side is the cerebellum, *B* (Fig. 73), consisting of a *right,* a *left,* and a *median lobe;* on the ventral side is the *pons Varolii, C* (Fig. 73), and behind that the *medulla oblongata, D* (Fig. 73), which is continuous with the spinal cord.

In nature, the main divisions of the brain are not separated so much as has been represented in the diagram for

Cb

Mo

Fig. 74.—The brain from the left side. *Cb,* the cerebral hemispheres forming the main bulk of the fore-brain; *Cbl,* the cerebellum ; *Mo,* the medulla oblongata; *P,* the pons Varolii ;* the fissure of Sylvius.

the sake of clearness, but lie close together, as represented in Fig. 74, only some folds of the membranes extending between them ; and the mid-brain is entirely covered in on its dorsal aspect. Nearly everywhere the surface of the brain is folded, the folds, known as *gyri* or *convolutions* being deeper and more numerous in the brain of man than in that of the animals nearest allied to him; and in the human species more marked in the higher than in the lower races. It should however be added that some species of animals

which are not markedly intelligent have much convoluted cerebral hemispheres.

The brain like the spinal cord consists of gray and white nervous matter, but somewhat differently arranged, for while the brain, like the cord, contains gray matter in its interior, a great part of its surface is also covered with it. By the external convolutions of the cerebellum and the cerebral hemispheres the surface over which this gray substance is spread is very much increased (see Fig. 74).

The Ventricles of the Brain. The minute central canal of the spinal cord is continued into the brain and expands

Fig. 75.—Diagram of the right half of a vertical median section of the brain. *H, H,* convoluted inner surface of right cerebral hemisphere, *5,* the fifth ventricle; the figure is placed on the thin inner wall of the right lateral ventricle; *Cc, corpus callosum; 3,* the third ventricle ; the partition separating it from the fifth ventricle is the *fornix,* and just behind the anterior thickened end of the *fornix* is shown part of the right foramen of Monro *m,* leading to the right lateral ventricle ; *t,* the soft commissure cut across; in the fore part of the *fornix* is the anterior commissure; the anterior portion of the floor of the third ventricle shows two downward prolongations, one directed to the optic commissure, *z,* the other (*infundibulum*) to the pituitary body, *pt; a,* the pineal body; the thickening immediately beneath its root is the posterior commissure; the mass forming the exposed wall of the ventricle and on which the figure 3 is placed is the inner side of the right optic thalamus ; *o, d,* the anterior and posterior *corpora quadrigemina* of the right side; *4,* the fourth ventricle lying near the dorsal side of the *medulla oblongata, Mo,* and connected by the *iter* with the third ventricle; posteriorly it is continued to join the central canal of the spinal cord; *Cr,* right *crus cerebri ; P, pons Varolii; Cb, cerebellum;* where it is divided in the middle line the radial arrangement of its central white matter forming the so-called *arbor vitæ* is seen; *op* right optic nerve proceeding from the optic commissure ; *oc,* the third cranial nerve arising from the crus cerebri; *1,* callosal convolution.

there at several points into chambers known as the *ventricles.* Entering the medulla oblongata it approaches its upper surface and dilates into the *fourth ventricle,* 4, Fig. 75,

which has a very thin roof, lapped over by the cerebellum. From the front of the fourth ventricle runs a narrow passage (*aqueduct of sylvius* or *iter*) which enters another dilatation, 3, Fig. 75, lying in the middle line near the under side of the fore-brain and known as the *third ventricle*. From the third ventricle two apertures (the foramens of Monro), one of which is partly seen at *m* in the diagram, lead into the *first* and *second*, or *lateral ventricles*, one of which lies in each of the cerebral hemispheres. The front ends of these two ventricles are seen in the vertical transverse section of the brain represented in Fig. 76.
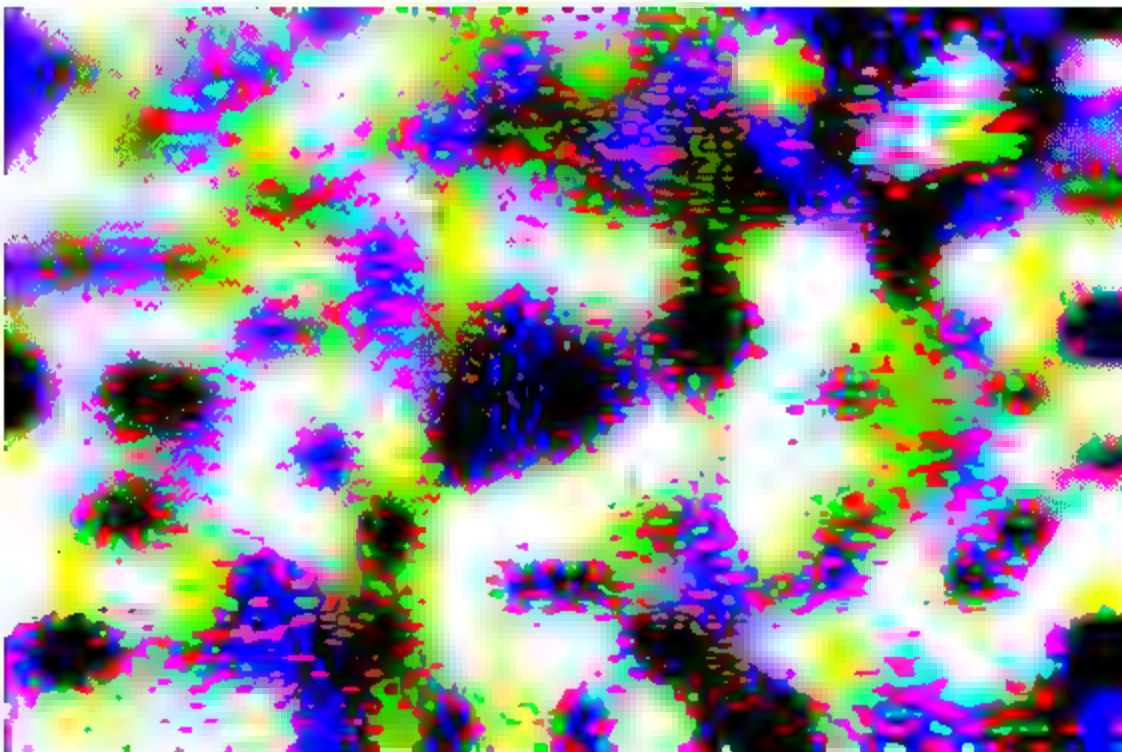
FIG. 76.—A vertical section across the cerebral hemispheres taken in front of the fifth ventricle. *Ccl²*, anterior part of *corpus callosum* , *VI*, the anterior end of the right lateral ventricle; the gray mass on its exterior is the front end of the *corpus striatum*. On the left side the superficial gray matter covering the convolutions is shaded.

The ventricles contain a small amount of *cerebro-spinal liquid*, and are lined by epithelium which is ciliated in early life. Part of the posterior wall of the third ventricle is extremely thin, consisting of little but this epithelium supported by a thin layer of pia mater: this part is pushed in or doubled into the cavity of the ventricle in the form of a triangular membrane, the *velum interpositum*, which lies beneath the fornix and sends offshoots into the lateral ventricles. Between the upper and lower layers of the induplicated velum interpositum arteries enter and there break up into plexuses—the *choroid plexuses*—covered everywhere by

the pushed-in epithelium. These plexuses occupy a considerable part of the third and lateral ventricles: and a pair of similar vascular tufts drive in before them part of the thin roof of the fourth ventricle and encroach on its cavity.

Note. A frequent cause of *apoplexy* is a hemorrhage into one of the lateral ventricles; the outpoured blood accumulating and pressing upon the cerebral hemispheres, their functions are suppressed and unconsciousness produced. When a person is found in an apoplectic fit therefore the best thing to do is to leave him perfectly quiet until medical aid is obtained: for any movement may start afresh a bleeding into the ventricle which had been stopped by clots formed in the mouths of the torn blood-vessels.

Sections of the Brain. Having got a general idea of the parts composing the brain, the best way to continue the study of its anatomy is to examine sections taken in various directions. Two such are given in Figs. 75 and 76. Fig. 75 represents the right half of a vertical section of the brain, taken from before back in the middle line and viewed from the inner side. Above, the knife has passed between the two cerebral hemispheres, in the longitudinal fissure, without cutting either, and the convoluted inner surface of the right one is seen. The sickle-shaped mass lower down, *Cc* to *Cc*, represents the cut surface of a connecting band of white nervous tissue called the *corpus callosum*, which runs across the middle line from one cerebral hemisphere to the other and puts them in communication. Beneath the corpus callosum the knife has opened a cavity, the *fifth ventricle*, 5, bounded on each side by a very thin wall, which forms part of the inner wall of the corresponding lateral ventricle; the median partition formed by these two walls and containing the slit-like fifth ventricle is the *septum lucidum*. The fifth is quite different in origin from the remaining cerebral ventricles, not being a continuation of the canalis centralis of the spinal cord.

Forming the floor of the fifth ventricle and separating it from the *third ventricle*, 3, is the *fornix*, mainly made up of fibres running from before back. The anterior downward-curved end of the fornix is thickened, and contains the anterior *commissure*, a small cord of transverse nerve-fibres. The cavity of the third ventricle is narrow from side to side, and is bounded laterally by the *optic thalami*, of which the

right, having the figure 3 placed on it, has its median side exposed in the section. The third ventricle is crossed about its middle by the *middle commissure, t,* and from its anterior end the foramina of Monro, of which the right, *m,* is partly exposed in the section, lead to the lateral ventricles. From the fore part of the third ventricle two conical extensions pass downward, one directed to *z,* the *optic commissure,* from which the optic nerves pass, and the other, named the *infundibulum,* to the *pituitary body, pt.* The latter consists of an anterior and posterior lobe, and in the human brain contains no nervous elements. The anterior lobe, indeed, is an outgrowth from the pharynx of the embryo, and only secondarily becomes attached to the brain. It is not known to have any function in existing vertebrates. From the posterior part of the floor of the third ventricle the *iter* leads as a narrow passage dorsal to the *crura cerebri, Cr,* and ventral to the *corpora quadrigemina, o, d,* to the *fourth ventricle,* 4. Projecting from the posterior wall of the third ventricle is a small conical non-nervous mass, the *pineal body,* which, though of no functional importance, is of interest, in the first place because the philosopher Descartes considered it the special seat of the soul, and in the second because embryology and comparative anatomy show that it is the remnant of a third median eye, which primitive vertebrates possessed on the dorsal side of the head. In some existing reptiles its original structure is more complete than in man, but in none is it functional. Just beneath the attachment of the pineal body is a slight thickening of the posterior wall of the third ventricle containing transverse fibres, and named the *posterior commissure.* The third ventricle and the parts immediately surrounding it constitute the *inter-brain* or *thalamencephalon,* which with the two cerebral hemispheres and the corpus callosum and fornix makes up the fore brain.

The mid-brain, consisting mainly of the *crura cerebri, Cr,* and the corpora quadrigemina, *o, d,* and traversed by the narrow iter, is continuous posteriorly with the hind brain, consisting of *pons Varolii, P; cerebellum, Cb;* and *medulla oblongata, Mo.* The thin-roofed cavity of the fourth ventricle, 4, lies near its dorsal side. Where cut in making the section the cerebellum shows a curious branching core of white nerve matter, surrounded by gray, named *arbor vitæ* by the old anatomists. The pons consists mainly of transverse fibres

uniting the right and left halves of the cerebellum; the medulla oblongata and crura contain mainly longitudinal fibres, but there are many transverse.

Fig. 76 represents a vertical transverse section of the brain taken through the fore part of the corpus callosum (*Ccl*) and altogether in front of the third ventricle. It shows the foldings of the cerebrum and its superficial layer of gray substance; the anterior ends of the lateral ventricles, *VI*, with a gray mass, the *corpus striatum* lying beneath and on the outer side of each. If the section had been taken a little farther back the *optic thalami* would have been found reaching the floor of each ventricle. Like the optic thalamus, to the front of and partly to the outer side of which it lies, the corpus striatum is mainly composed of gray nerve matter. It is, however, divided in its posterior region into an inner and outer portion by a well marked band of white substance, consisting of nerve fibres, passing through on the way to or from the surface of the cerebral hemispheres: this band is the *internal capsule*.

The Base of the Brain and the Cranial Nerves. Twelve pairs of nerves leave the skull by apertures in its base, and are known as the cranial nerves. Most of them spring from the under side of the brain, and so they are best studied in connection with the base of that organ, which is represented in Fig. 77. The *first pair*, or *olfactory nerves*, spring from the under sides of the olfactory lobes, *I*, and pass out through the roof of the nose. They are the nerves of smell. The *second pair*, or *optic nerves*, *II*, spring from the optic thalami and corpora quadrigemina, and, under the name of *optic tracts*, run down to the base of the brain, where they appear passing around the crura cerebri, as represented in the figure. In the middle line the two optic tracts unite to form the *optic commissure* (seen in section at *z*, in Fig. 75), from which an optic nerve proceeds to each eyeball. Behind the optic commissure is seen the conical stalk of the *pituitary body* or *hypophysis cerebri* (*pt* in Fig. 75), and still further back a pair of hemispherical masses, about the size of split peas, known as the *corpora albicantia*.

All the remaining cranial nerves arise from the hindbrain. The third pair (*motores oculi*) arise from the front of the pons Varolii, and are distributed to most of the muscles which move the eyeball and also to that which lifts the upper eyelid. The four-sided space bounded by the optic tracts

and commissure in front and the third pair of nerves behind, and having on it the pituitary body and the corpora albicantia, lies beneath the third ventricle, so that a probe pushed in there would enter that cavity (see Fig. 75).

Fɪɢ. 77.—The base of the brain. The cerebral hemispheres are seen overlapping all the rest. *I,* olfactory lobes; *II,* optic tract passing to the optic commissure from which the optic nerves proceed; *III,* the third nerve or *motor oculi; IV,* the fourth nerve or *patheticus; V,* the fifth nerve or *trigeminalis; VI,* the sixth nerve or *abducens; VII,* the seventh or facial nerve or *portio dura; VIII,* the auditory nerve or *portio mollis; IX,* the ninth or glosso-pharyngeal; *X,* the tenth or pneumogastric or *vagus; XI,* the spinal accessory, *XII,* the hypoglossal; *ncI,* the first cervical spinal nerve.

The fourth pair of nerves, *IV* (*pathetici*), arise from the front part of the roof of the fourth ventricle. From there, each curls around a *crus cerebri* (the cylindrical mass seen beneath it in the figure, running from the pons Varolii to enter the under surface of the cerebral hemispheres) and appears on the base of the brain. Each goes to one muscle of the eyeball.

The fifth pair of nerves (*trigeminales*), *V,* resemble the

spinal nerves in having two roots; one of these is much larger than the other and possesses a ganglion (the *Gasserian ganglion*) like the dorsal root of a spinal nerve. Beyond the ganglion the two roots form a common trunk which divides into three main branches. Of these, the *ophthalmic* is the smallest and is mainly distributed to the muscles and skin over the forehead and upper eyelid; but also gives branches to the mucous membrane lining the nose, and to the integument over it. The second division (*superior maxillary nerve*) of the trigeminal gives branches to the skin over the temple, to the cheek between the eyebrow and the angle of the mouth, and to the upper teeth; as well as to the mucous membrane of the nose, pharynx, soft palate and roof of the mouth. The third division (*inferior maxillary*) is the largest branch of the trigeminal; it receives some fibres from the larger root and all of the smaller. It is distributed to the side of the head and the external ear, the lower lip and lower part of the face, the mucous membrane of the mouth and the anterior two thirds of the tongue, the lower teeth, the salivary glands, and the muscles which move the lower jaw in mastication.

The *sixth pair* of cranial nerves (Fig. 77), *VI*, or *abducentes* arise from the posterior margin of the pons Varolii, and each is distributed to one muscle of the eyeball.

The *seventh pair* (*facial nerves*), *VII*, appear also at the posterior margin of the pons. They are distributed to most of the muscles of the face and scalp.

The *eighth pair* (*auditory nerves*) arise close to the facial. They are the nerves of hearing and are distributed entirely to the internal ear.

The *ninth pair* (*glossopharyngeals*), *IX*, arising close to the auditories, are distributed to the mucous membrane of the pharynx, the posterior part of the tongue, and the middle ear.

The *tenth pair* (*pneumogastric nerves* or *vagi*), *X*, arise from the sides of the medulla oblongata. Each gives branches to the pharynx, gullet and stomach, the larynx, windpipe and lungs, and to the heart. The vagus runs farther through the body than any other cranial nerve.

The *eleventh pair* (*spinal accessory nerves*), *XI*, do not arise mainly from the brain but by a number of roots attached to the lateral columns of the cervical portion of the spinal

cord, between the anterior and posterior roots of the proper cervical spinal nerves. Each, however, runs into the skull cavity alongside of the spinal cord and, getting a few filaments from the medulla oblongata, passes out along with the glossopharyngeal and pneumogastric nerves. Outside the skull it divides into two branches, one of which joins the pneumogastric trunk, while the other is distributed to muscles about the shoulder.

The *twelfth pair* of cranial nerves (*hypoglossi*), *XII*, arise from the sides of the medulla oblongata; they are distributed mainly to the muscles of the tongue and hyoid bone.

Deep Origins of the Cranial Nerves. The places referred to above, at which the various cranial nerves appear on the surface of the brain, are known as their superficial origins. From them the nerves can be traced for a lesser or greater way in the substance of the brain until each is followed to one or more masses of gray matter, which constitute its proper starting-point and are known as its *deep origin*. The deep origins of all except the first and second and part of the eleventh lie in the medulla oblongata, midbrain, and thalamen cephalon.

The Ganglia and Communications of the Cranial Nerves. Besides the Gasserian ganglion above referred to, many others are found in connection with the cranial nerves. Thus for example there is one on each of the main divisions of the trigeminal, two are found on each pneumogastric and two in connection with the glossopharyngeal. At these ganglia and elsewhere, the various nerves often receive branches from neighboring cranial or spinal nerves, so that very soon after it leaves the brain hardly any, except the olfactory, optic, and auditory, remains free from fibres derived from other trunks. This often makes it difficult to say from where the nerves of a special part have come; for example, the nerve-fibres going to the submaxillary salivary gland from the trigeminal leave the brain first in the facial and only afterwards enter the fifth; and many of the fibres going apparently from the pneumogastric to the heart come originally from the spinal accessory.

The Sympathetic System. The ganglia which form the main centres of the sympathetic nervous system lie in two rows (*s*, Fig. 2, and *sy*, Fig. 3), one on either side of the bodies of the vertebræ. Each ganglion is united by a nerve-trunk with the one in front of it, and so two great chains are

formed reaching from the base of the skull to the coccyx. In the trunk region these chains lie in the ventral cavity, their relative position in which is indicated by the dots *sy* in the diagrammatic transverse section represented on p. 6 in Fig. 3. The ganglia on these chains are forty-nine in number, viz., twenty-four pairs, and a single one in front of the coccyx in which both chains terminate. They are named from the regions of the vertebral column near which they lie; there being three cervical, twelve thoracic, four lumbar, and five sacral pairs.

Each sympathetic ganglion is united by *communicating branches* with the neighboring spinal nerves, and near the skull with various cranial nerves also; while from the ganglia and their uniting cords arise numerous trunks, many of which, in the thoracic and abdominal cavities, form plexuses, from which in turn nerves are given off to the viscera. These plexuses frequently possess numerous ganglia of their own; two of the most important are the *cardiac plexus* which lies on the dorsal side of the heart, and the *solar plexus* which lies in the abdominal cavity and supplies nerves to the stomach, liver, kidneys, and intestines. Many of the sympathetic nerves finally end in the walls of the blood-vessels of various organs. To the naked eye they are commonly grayer in color than the cerebro-spinal nerves.

The Sporadic Ganglia. These are found scattered in nearly all parts of the Body except the limbs. They are for the most part small, even microscopic in size, though several large ones exist in the abdominal cavity. They are especially abundant in the neighborhood of secretory tissues and about blood-vessels, while a very important set is found in the heart. Nerves unite them with the cerebro-spinal and sympathetic centres, and probably most of them should be classified as belonging to the sympathetic system.

The Histology of Nerve-Fibres. The microscope shows that in addition to connective tissue and other accessory parts, such as blood-vessels, the nervous organs contain tissues peculiar to themselves and known as *nerve-fibres* and *nerve-cells*. The cells are found in the centres only; while the fibres, of which there are two main varieties known as the *white* and the *gray*, are found in both trunks and centres; the white variety predominating in most cerebro-spinal nerves and in the white substance of the centres, and the

gray in the sympathetic trunks and the gray portions of the central organs.

If an ordinary cerebro-spinal nerve-trunk be examined it will be found to be enveloped in a loose sheath of areolar connective tissue, which forms a packing for it and unites it to neighboring parts. From this sheath, or *perineurium,* bands of connective tissue penetrate the nerve and divide it up into a number of smaller cords or *funiculi,* much as a muscle is subdivided into fasciculi; each funiculus has a sheath of its own called the *neurilemma,* composed of several

FIG. 78.   FIG. 79.

FIG. 78.—White nerve-fibres soon after removal from the Body and when they have acquired their double contour
FIG. 79.—Diagram illustrating the structure of a white or medullated nerve-fibre. 1, 1, primitive sheath; 2, 2, medullary sheath; 3, axis cylinder.

concentric layers of a delicate membrane, within which the true nerve-fibres lie. These, which would be nearly all of the white kind, consist of extremely delicate threads, on the average, 0.0125 mm. ($\frac{1}{2000}$ inch) in diameter, though often considerably smaller, and of a length which is in proportion very great. The core of each nerve-fibre in fact is continuous from a nerve-centre to the organ in which it ends, so that the fibres, e.g., which pass out through the sacral plexus and then run on through the sciatic nerve and its branches to the skin

of the toes, are three to four feet long. If a fresh *white nerve-fibre* be examined with the microscope it presents the appearance of a perfectly homogeneous glassy thread; but soon it acquires a characteristic double contour (Fig. 78) from the coagulation of a portion of its substance. By proper treatment with reagents three layers may be brought into view. Outside is a fine transparent envelope (1, Fig. 79) called the *primitive sheath*; inside this is a fatty substance, 2, forming the *medullary sheath* (the coagulation of which gives the fibre its double border), and in the centre is a core, the *axis cylinder*, 3, which is longitudinally fibrillated and is clearly the essential part of the fibre, since near the ending the primitive and medullary sheaths are frequently absent. At intervals of about one millimeter ($\frac{1}{25}$ inch) along the fibre are found *nuclei* (c, Fig. 80), around each of which lies a little protoplasm. These are indications of the primitive cells which have elongated and formed an envelope for the axis cylinder, which itself is a branch given off by a nerve-cell in some centre. The medullary sheath is interrupted half-way between each pair of nuclei at a point called the *node of Ranvier* (R, Fig. 80), which is the boundary between two of the enveloping cells. In the course of a nerve-trunk its fibres rarely divide; when a branch is given off some fibres merely separate from the rest, much as a skein of silk might be separated out at one end into smaller bundles containing fewer threads. Near their ends, however, nerve-fibres frequently branch, and then a division of the axis cylinder goes to each branch.

A   B

Fig. 80.—Portions of two *white* or *med- ullated nerve-fibres,* magnified more than four hundred diame- ters: they have been treated with osmic acid which stains the medullary sheath black and brings in- to view the nuclei, c, c, and nodes of Ranvier R. The axis cylinder is seen to be continuous through the nodes.

Gray Nerve-Fibres. Some of these are merely white fibres which near their peripheral ends have lost their medullary sheaths; others have no medullary sheath throughout their whole course, and consist merely of an axis cylinder (often striated) and nuclei, with

or without a primitive sheath. Such fibres are especially abundant in the sympathetic trunks; and they alone form the olfactory nerve. In the communicating branches between the sympathetic ganglia and the spinal nerves both white and gray fibres are found; the former are cerebro-spinal fibres passing into the sympathetic system, while the gray fibres originate in the sympathetic system and pass to the membranes and blood-vessels of the spinal cord and spinal column. Another group of gray nerve-fibres may be called *nerve-fibrils:* they are extremely fine, and result from the subdivision of axis cylinders, close to their final endings in many parts of the Body, after they have already lost both primitive and medullary sheaths. Many fine gray fibres exist in the nerve-centres.

The Histology of Nerve-Cells. The only structures known with certainty to be connected with the central ends of nerve-fibres are *nerve-cells,* and so many nerve-fibres have
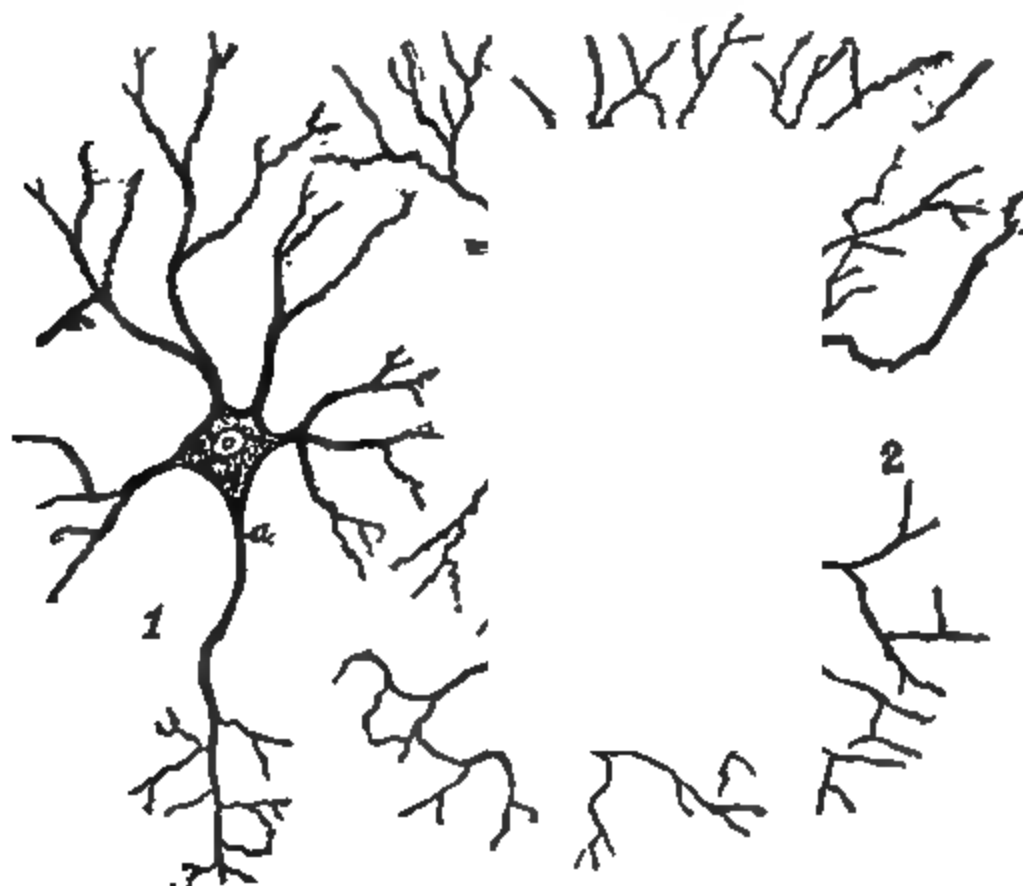
Fig. 61.—Nerve-cell from anterior horn of grey matter of spinal cord; *a,* axis-cylinder process. 2, Cell from posterior horn of spinal cord.

been traced into continuity with nerve-cells, that it is fairly certain all arise in this way. The latter may therefore be regarded as the central organs of the nerve-fibres.

At 1, Fig. 81, is shown a typical nerve-cell such as may be found in an anterior horn of the gray matter of the spinal cord. It consists of the *cell body,* or cell protoplasm, in which is a large *nucleus* containing a *nucleolus.* From the body of the cell arise several branches, the great majority of which are granular and divide frequently in a forking or *"dichotomous"* manner. These are known as the *"protoplasmic "* branches of the cell, and possibly serve merely to absorb nourishment for it. One branch, however, *a,* gives off at right angles smaller filaments, but still maintains its individuality and ultimately becomes the axis cylinder of a nerve-fibre. Its side branches probably put it in anatomical continuity with other nerve-fibres and other nerve-cells. Nerve cells from the posterior horn of the grey matter of the spinal cord (2, Fig. 81) also possess numerous granular protoplasmic processes and a nerve-fibre process (*b*); but the latter, instead of continuing directly into an axis cylinder, breaks up into a network of fine branches which frequently unite with one another and also, no doubt, with fibrils from neighboring cells. It is almost certain that one or more of these fibrils or a bunch of them forms the axis cylinder of a fibre in a dorsal root of a spinal nerve.

As we shall learn later, the dorsal roots are concerned in carrying impulses from the skin and other sensitive parts to the spinal cord; the anterior roots in conveying impulses from the nerve-centres to the organs (muscles, glands, etc.) of the Body. Therefore, in general terms, we may speak of the type of nerve-cell 1, Fig. 81, as a motor nerve-cell; and the type of cell 2, Fig. 81, as a sensory nerve-cell. Both varieties of cells are found abundantly in the gray matter of the brain (Fig. 83), along with other forms, of which the pear-shaped *cells of Purkinje* existing in the cerebellum may be mentioned (Fig. 82).

In the sympathetic and sporadic ganglia somewhat simpler forms of nerve-cells, having fewer branches, occur. As a rule nerve-cells are comparatively large and have conspicuous nuclei, but in the brain many small ones exist.

Neuroglia. In the brain and spinal cord the true nervous elements are intertwined with and supported by connective tissue and minute blood-vessels, but in addition there is found closely twisted around the cells and fibres a peculiar tissue

made of greatly branched cells (Fig. 83), and named the *neuroglia* or *sustentacular tissue.*

Nerve-Centres consist of white and gray nerve-fibres, of nerve-cells, of neuroglia, and of connective tissue and blood-vessels arranged in different ways in the different centres. They are essentially collections of nerve-

Fig. 82.—A thin section of the cerebellum showing pear-shaped cells of Purkinje. and numerous other small nerve-cells.

Fig. 83.—Cells from the surface gray matter of a cerebral convolution *p*, nerve-cells with axis cylinder processes, *o* ; *n*, non-nervous neuroglia cells. The method of preparation (Golgi's) stains the cells an uniform black.

cells and nerve-fibres, some of the latter being connected with the cells, while others may merely pass through on their way to or from other centres. As an illustration of the structure of a more complex nerve-centre we may study the spinal cord.

Histology of the Spinal Cord. If a thin transverse section of the spinal cord be examined with a microscope it will be found that enveloping the whole is a delicate layer of connective tissue, the *pia mater.* Fine bands of it ramify

through the cord, supporting the nervous elements; some of
the coarser of these are represented at 6, 7, and elsewhere in
Fig. 84, but from these still finer processes arise, as represented
at *d* and *e* in Fig. 85. The ultimate finest tissue directly
supporting the nervous elements directly, is the *neuroglia.*
In the white columns, the cord (Fig. 85) will be seen to be

Fig. 84.—A thin transverse section of half of the spinal cord magnified about
10 diameters. 1, anterior fissure ; 2, posterior fissure ; 3, *canalis centralis*; 8, pia
mater enveloping the cord ; 6, 7, bands of pia mater penetrating the cord and sup-
porting its nerve elements ; 9, a posterior root ; 10, bundles of an anterior root ; *a*,
b, *c*, *d*, *e*, groups of nerve-cells in the gray matter.

mainly made up of medullated nerve-fibres which run longi-
tudinally and therefore appear in the transverse section as
circles, with a dot in the centre, which is the axis cylinder.
At *b* in Fig. 85 these fibres are represented, the intermediate
connective tissue being omitted, while at *e* this latter alone is
represented in order to show more clearly its arrangement.
At the levels of the nerve-roots horizontal white fibres are
found (9 and 10, Fig. 84, and *a*, Fig. 85), running into the
gray matter, and others exist at the bottom of the anterior
fissure, running from one side of the cord to the other. In

the gray substance the same supporting network of connective tissue is found, but in it the majority of the nerve-fibres are non-medullated, and at certain points nerve-cells, such as are totally absent in the white substance, are found. One collection of these nerve-cells is seen at *c* in Fig. 84, and others are represented at *a, e, f*, and elsewhere. The nerve-fibres in the gray matter are for the most part branches of the axis cylinder processes of these cells (see Fig. 81), and as they unite with one another freely they form a structurally continuous network through the whole gray substance. The fibres of the anterior roots of the spinal nerves enter the gray matter and there most of them soon become continuous with the axis cylinder process of a nerve-cell; the ending of the posterior root-fibres is not quite certain, but they appear to break up and join the gray network, to be by it placed indirectly in connection with nerve-cells. In any case the fundamental fact remains that every nerve-fibre joining the spinal cord is directly or indirectly in continuity with the gray network, and so with all the other fibres of all the spinal nerves.

Fɪɢ. 85.—A small bit of the section represented in Fig. 84 more magnified. *a,* a bundle of fibres from an anterior root passing through the white substance on its way to the gray. Towards the right of the figure the nerve-fibres of the anterior column have been omitted so as to render more conspicuous the supporting connective tissue, *d* and *e*. Elsewhere the nerve-fibres alone are represented; *c,* enveloping *pia mater*. The neuroglia is not indicated.

From the sides of the gray substance, fibres continually pass out into the white portion and become medullated; some of these enter the gray network again at another level and so bring parts of the cord into especially close union, while others pass on into the brain. At the top of the neck, moreover, the gray matter of the cord is continuous with that of

the medulla oblongata and through it with the rest of the brain, so that nervous disturbances can pass by anatomically continuous paths from one to the other.

The Structure of a Spinal Ganglion. When one of these ganglia is cut lengthwise, and the section examined microscopically, it is seen that connective tissue forms an envelope for it, and sends ramifying bundles through it. The fibres of the posterior root become separated into bundles when they enter a ganglion and unite into a single bunch when they leave it to join the mixed spinal nerve trunk. Between the bundles of nerve-fibres within the ganglion are groups of nerve-cells, and probably each fibre on its way through the ganglion is connected with a cell. This connection occurs in a somewhat peculiar way. The cells (Fig. 86) are pear-shaped, granular,

Fig. 86.—Diagram of a spinal ganglion cell : *ac*, its fibrillated process, which acquiring primitive sheath, *ps*, and medullary sheath, *ms*, becomes a fibre which at the node of Ranvier *nr* joins a posterior root fibre, part of its axis cylinder, *c*, running centrally in this, and part, *d*, distally.

contain a large nucleus and nucleolus, and average $\frac{1}{15}$ mm. ($\frac{1}{150}$ inch) in long diameter. Near its narrow end the cell substance is fibrillated, and a bundle of these fine fibres, *ac*, passes from it, something like the stalk from a pear. This stalk is an axis cylinder, and has on it small nuclei. A little way from the cell the axis cylinder acquires a primitive sheath, *ps*, and a little farther on a medullary sheath, *ms*, so that it becomes a fully formed white nerve-fibre. At a node of Ranvier (usually that one nearest the cell), *nr*, this divides, its branches diverging from it at right angles: one branch runs to the posterior root and enters the spinal cord; the other continues through the ganglion as a fibre of the mixed nerve-trunk. The axis cylinders of these branches, *c* and *d*, in some cases at least, contain fibrillæ not derived from the pear-shaped cell in addition to those which are. Each cell as it lies in the ganglion is encased in a delicate envelope of

flattened nucleated cells (not indicated in the figure), probably belonging to the surrounding connective tissue. Blood-vessels are distributed in the ganglion, the capillaries being especially numerous about the nerve-cells.

Most of the cells of sympathetic and other peripheral ganglia seem to have several branches, no one of which differs essentially from the rest; probably each branch becomes part of the axis cylinder of a different fibre, the cell thus placing several distinct fibres in communication.

CHAPTER XIII.

THE GENERAL PHYSIOLOGY OF THE NERVOUS SYSTEM.

The Properties of the Nervous System. *General Considerations.* If the finger of any one unexpectedly touches a very hot object, pain is felt and the hand is suddenly snatched away; that is to say, sensation is aroused and certain muscles are caused to contract. If, however, the nerves passing from the arm to the spinal cord have been divided, or if they have been rendered incapable of activity by disease, no such results follow. Pain is not then felt on touching the hot body nor does any movement of the limb occur; even more, under such circumstances the strongest effort of the will of the individual is unable to bring about movement of his hand. If, again, the nerves of the limb have uninjured connection with the spinal cord, but parts of the latter, higher up, between the brain and the point of junction of the nerves of the brachial plexus with the cord, are injured, then a sudden contact with the hot body will cause the arm to be snatched away, but no pain or other sensation due to the contact will be felt, nor can the will act upon the muscles of the arm. From the comparison of what happens in such cases (which have been observed over and over again upon wounded or diseased persons) with what occurs in the natural condition of things, several important conclusions may be arrived at:

1. *The feeling of pain does not reside in the burnt part itself;* although that may be perfectly normal, no sensation will be aroused by any external force acting upon it, if the nervous cords uniting it with the centres be previously divided.

2. *The hot body has originated some change which, when propagated along the nerve-trunks, has excited a condition of the nerve-centres which is accompanied by a sensation,* in this particular case a painful one. This is clear from the fact that the loss of sensation immediately follows division of the

nerves of the limb, but not the injury of any of its other parts; unless of such a character as to cut off the supply of blood, when of course the nerves soon die, with the rest. Even, however, some time after tying the vessels which carry blood to a limb one can observe in experiments upon the lower animals that sensibility is still retained if the nerves be not directly injured.

3. *When a nerve in the skin is excited by a burn, or otherwise, it does not directly call forth muscular contractions;* for if so, touching the hot body would cause the limb to be moved even when the nerve had been divided high up in the arm, and as a matter of observation and experiment we find that no such result follows if the nerve-fibres have been cut in any part of their course from the burned part to the spinal marrow. It is therefore *through the nerve-centres that the change transmitted from the excited part of the skin is reflected or sent back, to act upon the muscles.*

4. The last deduction makes it probable *that nerve-fibres must pass from the centre to muscles as well as from the skin to the centre.* This is confirmed by the fact that if the nerves of the limb be divided the will is unable to act upon its muscles, showing that these are excited to contract through the nerves. That the nerve-fibres concerned in arousing sensation and muscular contractions are different, is shown also by cases of disease in which the sensibility of the limb is lost while the power of voluntarily moving it remains, and by other cases in which the reverse is seen, objects touching the hand being felt while it cannot be moved by the will. We conclude then that certain nerve-fibres when stimulated convey something (*a nervous impulse*) to the centres, and that these when excited may radiate impulses through other nerve-fibres to distant parts, the centre serving as a connecting link between the fibres which carry impulses from without in, and those which convey them from within out.

5. Further we conclude *that the spinal cord can act as an intermediary between the fibres carrying-in nervous impulses and those carrying them out, but that sensations cannot be aroused by impulses reaching the spinal cord only, nor has the Will its seat there; volition and consciousness are dependent upon states of the brain.* This follows from the unconscious movements of the limbs which follow stimulation of its skin after such injury to the spinal cord as pre-

vents the further transmission of nervous impulses (showing that the cord is a *reflex centre*), and from the absence, in such cases, of sensation in the part whose nerves have been injured, and the loss of the power of voluntarily causing its muscles to contract.

6. Finally we conclude that *the spinal cord in addition to being a centre for reflex actions serves to transmit nervous impulses to and from the brain;* a fact which is confirmed by the histological observation that in addition to the nerve-cells, which are the characteristic constituents of nerve-centres, it contains the simply conductive nerve-fibres, many of which pass on to the brain. In other words, the spinal cord, besides containing fibres which enter it from and pass from it to peripheral parts, contains many which unite it to other centres; and others which connect the various centres in it, as those for the arms and legs, together. This is true not only of the spinal cord, but of the brain (which contains many fibres uniting different centres in it), and probably of all nerve-centres.

The Functions of Nerve-Centres and Nerve-Trunks. From what has been stated in the previous paragraphs it is clear that we may distinctly separate the nerve-trunks from the nerve-centres. The fibres serve simply to convey impulses either from without to a centre or in the opposite direction, while the centres conduct and do much more. Some, as the spinal cord, are merely *reflex centres* and have nothing to do with states of consciousness. A man with his spinal cord cut or diseased in the thoracic region will kick violently if the soles of his feet be tickled, but will feel nothing of the tickling, and if he did not see his legs would not know that they were moving. Reflex centres moreover do not act, as a rule, indifferently and casually, but rearrange the impulses reaching them, so as to produce a protective or in some way advantageous result. In other words, these centres, acting in health, commonly *co-ordinate* the incoming impulses and give rise to outward-going impulses which produce an apparently purposive result. The burnt hand or the tickled foot, in the absence of all consciousness, is snatched away from the irritant; and food chewed in the mouth excites nerves there which act on a centre which causes certain cells in the salivary glands to make and pour into the mouth more saliva. In addition to the reflex centres we have others, placed in the

brain, the excitation of which is accompanied in us by various states of consciousness, as sensations, emotions, and the will; concerning these *centres of consciousness* our physiological knowledge is still very incomplete; what we know about them is based rather on psychological than physiological observation. The brain also contains a great many important reflex centres, as that for the muscles of swallowing, an act which goes on perfectly without our consciousness at all. In fact if we pay attention to our swallowing we fail to perform it as well as if we let the nervo-muscular apparatus alone, as is illustrated by the difficulty many persons experience on *trying* to swallow a pill. To complete the statement of the functions of the nerve-centres we must probably add two other groups. The first of these is that of the *automatic centres*, which are centres excited not directly by nerve-fibres conveying impulses to them, but in other ways. For example the breathing movements go on independently of our consciousness, being dependent on stimulation of a nerve-centre in the brain by the blood which flows through it (see Chap. XXVII); and the beat of the heart is also much dependent (Chap. XVIII) upon nerve-centres, the excitant of which is unknown. The final group of nerve-centres is represented by certain sporadic sympathetic and cerebro-spinal ganglia which are not known to be either reflex, automatic, or conscious in function. They may be called *relay and junction centres*, since in them probably an impulse entering by one nerve-fibre excites a cell, which by its communicating branches arouses many others, and these then send out impulses by the many nerve-fibres connected with them. By such means a single nerve-fibre can act upon an extended region of the Body. In other cases it seems likely that a feeble nervous impulse reaching an irritable nerve-cell excites changes in this comparable to those produced in a muscle when it is stimulated; the cell is in fact a store of readily decomposable material which breaks down when stimulated through one branch, with the liberation of energy, the discharge of which takes the form of reinforced nerve impulses sent along other branches or one of them.

That nerve-cells are the seats of considerable metabolic changes is indicated by the abundant supply of blood always sent to regions where they are numerous: and that some of their material is used up, or undergoes katabolism, during their activity and is replaced by anabolic processes during

rest, can be demonstrated histologically. If the sensory nerves of one fore limb of an animal be left at rest and those of the other simultaneously excited for several hours, it will be found, at the end of that time, that the nuclei of many cells of the spinal ganglia of the brachial nerves on the stimulated side are shrunken and distorted when compared with those of the other side. But if some hours be suffered to elapse before the animal is killed and the ganglia examined, the nuclei of the cells on both sides will be found equally large and well rounded. In carrier-pigeons after a long flight and in wild sparrows shot at the close of day, the nuclei of the nerve-cells connected with the origin of motor nerve-fibres are found to be shrivelled, and the whole cell frequently diminished in size when compared with specimens taken from birds after a period of rest. In old age the nuclei of many nerve-cells are small and distorted, even after prolonged rest.

Nerve-trunks and the white portions of nerve-centres are sparsely supplied with blood and undergo but small and slow nutritive changes in health. Their activity appears to consist in the transmission of some molecular motion not affecting the nutrition and chemical composition of the fibre, and not using up its material.

Excitant and Inhibitory Nerves. The great majority of the nerve-fibres of the Body when they convey nervous impulses to a part arouse it to activity; they are *excitant fibres.* There is, however, in the Body another very important set which arrest the activity of parts and which are known as *inhibitory nerve-fibres.* Some of these check the action of central nervous organs, and others the work of peripheral parts. For instance, taking a pinch of snuff will make most persons sneeze; it excites centrally acting fibres in the nose, these excite a centre in the brain, and this in turn sends out impulses by motor fibres which cause various muscles to contract. But if the skin of the upper lip be pinched immediately after taking the snuff, in most cases the reflex act of sneezing, which the Will alone could not prevent, will not take place. The afferent impulses conveyed from the skin of the lip have " inhibited " what we may call the " sneezing centre;" and afford us therefore an example of inhibitory fibres checking a centre. On the other hand, the heart is a muscular organ which goes on beating steadily throughout life; but if certain branches of the pneumogastric

nerve going to it be excited, the beat of the heart will be stopped; it will cease to work and lie in a relaxed resting condition: in this we have an instance of an inhibitory nerve checking the activity of a peripheral organ.

Classification of Nerve-Fibres. Nearly all the nerve-fibres of the Body fall into one of two great groups corresponding to those which carry impulses to the centres and those which carry them out from the centres. The former are called *afferent* or *centripetal fibres,* and the latter *efferent* or *centrifugal.* Since the impulses reaching the centres through the afferent fibres frequently cause sensations they are often called *sensory fibres ;* and as many of those which carry out impulses from the centres excite movements, they are frequently called *motor fibres ;* but these last names are bad, since even excluding inhibitory nerves, many afferent fibres are not sensory and many efferent are not motor.

We may distinguish as subdivisions of *afferent fibres* the following groups. 1. *Sensory fibres proper,* the excitement of which is followed by a sensation when they are connected with their brain-centre, which sensation may or may not give rise to a voluntary movement. 2. *Reflex fibres,* the excitation of which may be attended with consciousness but gives rise to involuntary efferent impulses. Thus for example light falling on the eye causes not only a sensation, but also a narrowing of the pupil, which is entirely independent of the control of the will. No absolute line can, however, be drawn between these fibres and those of the last group: any sudden excitation, as an unexpected noise, will cause an involuntary movement, while the same sound if expected would cause a movement or not according as was *willed.* 3. *Excito-motor fibres.* The excitation of these when reaching a nerve-centre causes the stimulation of efferent fibres, but without the participation of consciousness. During fasting, for instance, bile accumulates in the gall-bladder and remains there until some semi-digested food passes from the stomach into the intestine. This is acid and stimulates nerves in the mucous membrane lining the intestine, and these convey an impulse to a centre, which in consequence sends out impulses to the muscular coat of the gall-bladder causing it to contract and expel its contents into the intestine: but of all this we are entirely unconscious. 4. *Centro-inhibitory fibres.* Whether these exist as a distinct class is at present doubtful. It may be that

they are only ordinary sensory or reflex fibres, and that the inhibition is due only to the interference of two impulses reaching a central organ at the same time and impeding or hindering the full production of the normal result of either.

In *efferent nerve-fibres* physiologists also distinguish several groups. 1. *Motor fibres*, which are distributed to the muscles and govern their contractions. 2. *Vaso-motor fibres.* These are not logically separable from other motor fibres; but they are distributed to the muscles of the blood-vessels, and by governing the blood-supply of various parts, indirectly produce such secondary results as entirely overshadow their primary effect as merely producing muscular contractions. 3. *Secretory fibres.* These are distributed to the cells of the Body which form various liquids used in it, as the saliva and the gastric juice, and arouse them to activity. The salivary glands, for instance, may be made to form saliva by stimulating nerves going to them, and the same is true of the cells which form the sweat poured out upon the surface of the Body. 4. *Trophic nerve-fibres.* Under this head are included nerve-fibres which have been supposed to govern the nutrition of the various tissues, and so to control their healthy life. It has been doubted if any such nerve-fibres exist as a distinct class, and no doubt many of the facts which have been cited to prove their existence are otherwise explicable. For instance, *shingles* is a disease characterized by an eruption on the skin along the line of certain nerves, oftenest those which run between the ribs; but it may be dependent upon disease of the vaso-motor nerves which control the blood-supply of the part. In other cases diseases ascribed to injury of trophic nerves have been shown to be due to injury of the sensory nerves of the part, which having lost its feeling, is exposed to injuries from which it would otherwise have been protected. There are, however, cases which seem to indicate a direct nutritive influence of the nervous system on the tissues; as for example the acute bedsores seen in some diseased states of the spinal cord and leading to extensive destruction of the skin in a very few hours; and there is direct experimental evidence to show that stimulation of the branches of the pneumogastric nerve going to the heart tends to restore that organ when exhausted, while stimulation of the sympathetic branches has a precisely opposite effect (see Chapter XVIII). There is also no doubt that each nerve-fibre depends for the maintenance

of its nutrition on a nerve-cell since, if divided in its course, the part separated from the cell rapidly degenerates. It might also be urged that secretory nerves are trophic nerves in the true sense of the word, since when excited they cause the secretory cells to live in a special way, and produce substances which when unacted upon by their nerves they do not form. But if we call secretory nerves trophic we must include also under that name all other efferent nerves; the nutritive processes going on in a muscular fibre when at work are different from those in the same fibre when at rest, and the same is true of all other cells the activity of which is governed by nerve-fibres. 5. *Peripherally-acting inhibitory nerves*, such as those which slow or stop the beat of the heart.

Intercentral Nerve-Fibres. These, which do not convey impulses between peripheral parts and nerve-centres, but connect one centre with another, form a final group in addition to efferent and afferent nerve-fibres. Many of them connect the sporadic and sympathetic ganglia with one another and with the cerebro-spinal centre, while others place different parts of this latter in direct communication; as for instance different parts of the spinal cord, the brain and the spinal cord, and the two halves of the brain. The paths taken by some of these *commissural* fibres will be stated in connection with the physiology of the brain and spinal cord.

General Table. We may physiologically classify nerve-fibres as in the following tabular form, which is founded upon the facts above stated.

Nerve-fibres.	Peripheral.	Afferent.	Sensory. Reflex. Excito-motor. Inhibitory.
		Efferent.	Motor. Vaso-motor. Secretory. Trophic. Inhibitory.
	Intercentral.	Exciting. Inhibitory.	

The Electrical Phenomena of Nerves. Under certain conditions electrical currents can be led off from living nerve-

trunks and studied by aid of a galvanometer: in all respects these currents correspond to those of muscle, except that they are feebler. A perfectly fresh uninjured nerve at rest is isolectric, and so is a completely dead nerve. A dying portion of a nerve is negative to a more normal portion, and in consequence, if electrodes be placed, one on the centre and the other on the cut end of a freshly-removed portion of nerve, a current will be found passing through the connecting wire from the central portion of the piece of nerve towards the peripheral. A region of nerve in activity, that is transmitting a nervous impulse, is electro-negative to a region at rest, other things being equal; accordingly, an *action-current* or *negative variation* can be demonstrated on nerves as on muscles; the electrical change starting from the point of stimulation and travelling along the trunk, to be found at a distant part at a time when it has gone from the place of its first appearance. The account of the similar phenomena in muscle (Chap. X) may be consulted for a fuller statement.

The Stimuli of Nerve-Fibres. Nerve-fibres, like muscular fibres, possess no automaticity; acted upon by certain external forces or *stimuli* they propagate a change, which is known as a *nervous impulse*, from the point acted upon to their ends; but they do not generate nervous impulses when left entirely to themselves. Normally, in the living Body the stimulus acts on a nerve-fibre at one of its ends, being either some change in a nerve-centre with which the fibre is connected (efferent nerves) or some change in an organ attached to the outer end of the nerve (afferent fibres). Experiment shows, however, that a nerve can be stimulated in any part of its course; that it is irritable all through its extent. If, for example, the sciatic of a frog be exposed in the thigh and divided, it will be found that electric shocks applied at the point of division to the outer half of the nerve stimulate the motor fibres in it, and cause the muscular fibres of the leg to contract: and similarly such shocks applied to the cut end of the central half irritate the afferent fibres in it, as shown by the signs of feeling exhibited by the animal. In ourselves, too, we often have the opportunity of observing that the sensory fibres can be stimulated in their course at some distance from their ends. A blow at the back of the elbow, at the point commonly known as the "funny bone" or the "crazy bone," compresses the ulnar nerve there against the

subjacent bone, and in addition to irritating the nerves of the skin at the point struck, starts nervous impulses which make themselves known by severe tingling pain referred to the little and ring fingers to which the ulnar nerve is distributed. This shows not only that the nerve-fibres can be irritated in their course as well as at their ends, but also that sensations do not directly tell us where a nerve-fibre has been excited. No matter where in its course an impulse causing sensation has been started, we irresistibly refer its origin to the peripheral end of the afferent nerve-fibre affected.

General and Special Nerve-stimuli. Certain external forces excite all nerve-fibres, and in any part of their course. These are known as *general nerve-stimuli;* others act only on the end-organs of nerve-fibres, and often only on one kind of end-organ, and hence cannot be made to excite all nerves: these latter are commonly known as *special nerve-stimuli,* In reality they are not properly nerve-stimuli at all; but only things which so affect the irritable tissues attached to the ends of certain nerve-fibres as to make these tissues in turn excite the nerves. For example, light itself will not stimulate any nerve, not even the optic: but in the eye it effects changes (perhaps of a chemical nature) by which nerve-stimuli are produced and these stimulate the optic nerve-fibres. The ends of the nerves in the skin are not accessible to light nor are the proper end organs on which the light acts present there, so light does not lead to the production of nervous impulses in them: but the optic nerve without its peculiar end-organs would be just as insensible to light as these are. Similarly the aerial vibrations which affect us as sounds do not stimulate directly the fibres of the auditory nerve. They act on terminal organs in the ear, and these then stimulate the fibres of the nerve of hearing, just as they would any other nerve which happened to be connected with them.

General Nerve Stimuli. Those known are : (1) *Electric currents.* An electric shock passed through any part of any nerve-fibre powerfully excites it. A steady current passing through a nerve does not stimulate it, but any sudden change in this, whether an increase or a decrease, does. A very gradual change in the amount of electricity passing through a nerve in a unit of time does not stimulate it. (2) *Mechanical stimuli.* Any sudden pressure or traction, as

a blow or a pull, will stimulate a nerve-fibre. On the other hand steady pressure, or pressure very slowly increased from a minimum, will not excite the nerve. *(3) Thermal stimuli.* Any sudden heating or cooling of a nerve, as for instance bringing a hot wire close to it, will stimulate; slow changes of temperature will not. (4) *Chemical stimuli.* Many substances which chemically alter the nerve-fibre stimulate before killing it; thus dipping the cut end of a nerve into a strong solution of common salt will excite it; very slow chemical change in a nerve fails to stimulate.

In the case of all these general stimuli it will be seen that as one condition of their efficacy they must act with considerable suddenness. On the other hand too transient influences have no effect. An electric shock sent for only 0.0015 of a second through a nerve does not stimulate it: apparently the inertia of the nerve molecules is too great to be overcome by so brief an action. So, also, strong sulphuric acid and some other liquids kill nerves immediately, altering them so rapidly that they die before being stimulated.

Special Nerve-stimuli. These as already explained act only on particular nerves, not because one nerve is essentially different from another, but because their influence is excited through special end-organs which are attached to some nerves. These stimuli are: (1) Changes occurring in central organs, of whose nature we know next to nothing, but which excite the efferent nerve-fibres connected with them. The remaining special stimuli act on afferent fibres through the sense-organs. They are: (2) Light, which by the intervention of organs in the eye excites the optic nerve. (3) Sound, which by the intervention of organs in the ear excites the auditory nerve. (4) Heat, which through end-organs in the skin is able, by very slight changes, to excite certain nerve-fibres: such slight changes of temperature being efficient as would be quite incapable of acting as general nerve-stimuli without the proper end-organs. (5) Chemical agencies, which when extremely feeble and incapable of acting as general stimuli can act as special stimuli through special end-organs in the mouth and nose (as in taste and smell) and probably in other parts of the alimentary tract, where very feeble acids and alkalies seem able to excite certain nerves, and reflexly through them excite movements or render active the cells concerned in making the digestive

liquids. (6) Mechanical stimuli when so feeble as to be inefficient as general stimuli. Pressure on the skin of the forehead or of the back of the hand, equal to .002 gram (.03 grain) can be felt through the end-organs of the sensory fibres there, but would be quite incapable of acting as a general stimulus if applied directly to the nerve-fibre.

It will be noticed as regards the special stimuli of afferent nerves that many of them are merely less degrees of general stimuli ; the end-organs in skin, mouth, and nose are in fact excited by the same things as nerve-fibres, but they are far more irritable. In the case of the higher senses, seeing and hearing, however, the end-organs seem to differ entirely in property from nerve-fibres, being excited by sonorous and luminous vibrations which, so far as we know, will in no degree of intensity directly excite nerve-fibres. To construct an end-organ capable of recognizing very slight pressures we may imagine that all that would be needed would be to expose directly a very delicate end-branch of the axis cylinder ; and this seems in fact to be the case in the nerves of the transparent exposed part of the eyeball, if not in some other parts of the external integument of the Body. But as axis cylinders are quite unirritable by light or sound a mere exposure of them would be useless in the eye or ear, and in each case we find accordingly a very complex apparatus developed, whose function it is to convert modes of motion which do not excite nerves into others which do. We might compare this apparatus to a fuse with a detonating cap attached ; the stimulus of a blow from a hammer which would not itself ignite the fuse, acting on the detonating material (representing an " end-organ ") causes it to give off a spark, and this in turn ignites the fuse which answers to the nerve-fibre.

Specific Nerve-energies. We have already seen that a nervous impulse propagated along a nerve-fibre will give rise to different results according as different nerve-fibres are concerned. Travelling along one fibre it will arouse a sensation, along another a movement, along a third a secretion. In addition we may observe readily that these different results may be produced by the same physical force when it acts upon different nerves. Radiant energy, for example, falling into the eye causes a sensation of sight, but falling upon the skin one of heat, if any. The different results which follow the stimulation of different nerves do not then depend upon

differences in the physical forces exciting them. This is still further shown by the fact that different physical forces acting upon the same nerve arouse the same kind of sensation. Light reaching the eye causes a sight sensation, but if the optic nerve be irritated by a blow on the eyeball a sensation of light is felt just as if actual light had stimulated the nerve-ends; and a similar result follows if an electric shock be sent through the eyeball and optic nerve. Different nerves excited by the same stimulus produce different results, and the same nerve excited by different stimuli gives the same result. How are these facts to be explained ?

The first explanation which suggests itself is that the various nerves differ in their properties : that electricity applied to a motor nerve causes a muscle to contract, and to the optic nerve a visual sensation, and to the lingual nerve a sensation of taste, because nervous impulses in the motor, optic, and lingual nerves differ from one another. This was the view held by the older physiologists; and that supposed peculiarity of a muscular nerve by which its irritation caused a muscular contraction, and that of of the optic nerve in consequence of which its excitation caused a sensation of sight, and so on, they called the *specific energy of the nerve.* Seeing further that when a pure motor nerve was cut and its peripheral stump pinched the muscles connected with it contracted, but that when its central end was pinched no sensation or other recognizable change followed, while exactly the reverse was true of a sensory nerve, they believed that afferent nerves differed essentially from efferent nerves, inasmuch as the latter could only propagate impulses centrifugally and the former only centripetally. Now, however, we have much reason to believe that this view is wrong, and that all nerve-fibres, though perhaps exhibiting some minor differences, are essentially alike in their physiological properties, and can carry nervous impulses either way. The differences observed depend in fact not on any differences in the nerve-fibres, but on the different parts connected with their ends; that is to say, on the different terminal organs excited by the impulses conveyed by the fibre. A motor fibre is one which has at its peripheral end a muscular fibre, and a centrifugally travelling impulse reaching this will cause it to contract: but the cells connected with its central end are not of such a nature as to give rise to sensations

when centripetally travelling impulses reach them, or to transmit these. to other efferent fibres and so cause reflex movements; and therefore when a motor fibre is stimulated in the middle of its course the outward-going impulse causes a movement, while the centrally travelling impulse, starting at the same time, gives no direct sign of its existence. Similarly for a sensory nerve such as the ulnar, already referred to: if it be stimulated at the elbow the centrally travelling impulse will cause a sensation of pain by exciting the brain-centre connected with it, but the outward travelling impulse not reaching muscular fibres or other parts which it can arouse to activity, remains concealed from our notice. In other words, the so-called specific energy of a nerve-fibre depends upon the terminal organs on which it can act, and not on any peculiarity of the nerve-fibre itself.

Proofs that all Nerve-Fibres are Physiologically Alike. (1) The most marked difference between nerve-fibres is obviously that between efferent and afferent, and the microscope fails entirely to show any differences between the two. Some motor and some sensory fibres may be bigger or less than others, some may be white and others may be gray; but such differences are secondary, and have no direct relation to the function of a fibre as afferent or efferent. We can recognize no constant difference in structure between the two. (2) The physical properties and chemical composition of motor and sensory nerves agree in all known points. (3) When a nerve, say a motor one, is stimulated half-way between the centre and a muscle, a *nervous impulse,* as we call it, is propagated to the muscle, which impulse starts at the point stimulated and travels at a definite rate to the muscle, the contraction of which latter gives proof of its arrival. Now starting at the same moment from the same point, and travelling at the same rate, is that change in the electrical condition of the nerve which can be detected by a galvanometer, the so-called *negative variation* or *action current.* When a nerve is excited from its end-organ, as for example the optic nerve by light falling into the eyeball, or a motor nerve by a stimulus arising in a centre, an action current exactly like that observed with artificial stimulation travels along it. Since this negative variation always accompanies a nervous impulse, appearing when it appears and disappearing when it disappears, we conclude that it is a change

in the electrical properties of the nerve dependent on that internal movement of its molecules which constitutes a nervous impulse. It is an externally recognizable physical sign, and the only known one, of the existence of the nervous impulse while it is travelling along the fibre. If the muscle were cut away from the end of the nerve we could still detect that a nervous impulse had travelled from the point of stimulation to that where the fibres were divided, by tracking the negative variation. If, while stimulating a motor nerve half-way in its course, we examine galvanometrically the portion lying central to the stimulated point we find a well-marked centripetally travelling action current; it starts at the same moment as the efferent negative variation and travels in the same manner, but the nervous impulse of which it is a sign produces no more effect than the efferent impulse would after the muscle had been cut away; for it does not reach any muscular fibre, or sensory or reflex centre, which it can arouse to activity. Hence it is clear that the motor nerve can conduct impulses equally well in either direction; and similar experiment proves the same thing for pure sensory nerves.

While, however, by chemical or electrical stimulation of a motor or a secretory nerve we can get a muscular contraction or a secretion apparently quite identical with that produced by natural stimulation, we cannot make the same assertion with regard to afferent nerves. It is possible by gentle stimulation of a cutaneous afferent nerve through its end-organs in the skin to excite the centres, so that they in turn give rise to definitely combined reflex muscular contractions, producing, even in the absence of all consciousness, an useful movement. But if the skin be removed and the outer end of its afferent nerve stimulated directly, though the centres can be thus excited and caused to send out impulses to muscles, the movements which result are random kicks and jerks, very different from the definite, orderly movements which follow suitable stimulation through the skin. And as regards certain nerves of special sense something similar seems to be true. It has indeed been stated that mechanical injury of the optic nerve, as by cutting it during a surgical operation, causes a sensation of light in patients not anæsthized, but this has been denied; and though one positive observation counts for more in such a case than many negative, we must take into account the

fact that in no other sense-organ has the direct stimulation of the proper nerve-trunk in any other way than through the sense-organ at its outer end, been proved to give rise to true sensations of special sense. Stimulation of the nerves exposed in a wound does not cause a true touch sensation, but a feeling of pain; and similarly irritation of the trunks of the nerves of taste by diseased conditions does not seem to ever cause true taste sensations unless the end-organs in the mouth be also excited. Even if it turn out to be true that a nerve of special sense is only capable of giving rise to feelings belonging to the sphere of that sense when excited through its proper end-organs, that does not prove that its nerve-fibres have any unique faculty distinguishing them in property from other nerve-fibres. It only means that the brain organ, the central nerve-cell mechanism, to be excited by the nerve is highly complex, and only responds with the proper sensation when stimulated in proper strength and proper rhythm, and the sense organs accomplish this. Even the most delicate artificial stimulation that we can apply to a naked nerve-trunk is undoubtedly a crude and gross thing compared with the stimuli arising in the retina when light enters the eye, or in certain skin nerve end-organs when moderate heat falls on them. If we merely wish to get a noise out of a piano it does not matter how we strike it, if we strike hard enough ; and a muscular contraction or an irregular set of muscular contractions excited by direct stimulation of a nerve-trunk may be compared to such a noise. If we wish for a definite musical chord we must strike through the keyboard in a definite way; and the orderly combined muscular movements and the special sensations which follow stimulation through the proper sense-organs may be compared to such chords. In our bodies the keyboards are different in eye, ear, and skin, and adapted to be set in action by different external physical agencies, and the strings in connection with each keyboard are different and give different results; but the connecting apparatus, the nerve-fibre, lying between the keys in the sense-organs and the strings respectively responding to them in the centres, is essentially the same in all cases.

To put the case more definitely: Light outside the eye exists as ethereal vibrations, sound outside the ear as vibrations of the air (commonly). Each kind of vibration acts on

a particular end-organ in eye or ear which is adapted to be acted upon by it, and in turn these end-organs excite the optic and auditory nerve-fibres; these in consequence transmit impulses, which reaching different parts of the brain excite them; the excitement of one of these brain-centres is associated with sonorous and of the other with visual sensations. The nervous impulse in the two cases is quite alike, at least as to quality (though it may differ in quantity and rhythm) and the resulting difference in quality of the sensations cannot depend on it. The quality differences in these cases must be products of the central nervous system. If we had a set of copper wires we might by sending precisely similar electric currents through them produce very different results if different things were interposed in their course. In one case the current might be sent through water and decompose it, doing chemical work; in another, through the coil of an electro-magnet and raise a weight; in a third, through a thin platinum wire and develop light and heat; and so on, the result depending on the terminal organs, as we may call them, of each wire. Or, on the other hand, we might generate the current in each wire differently, in one by a Daniell's cell, in a second by a thermo-electric machine, in a third by the rotation of a magnet inside a coil, but the currents in the wires would be essentially the same, as the nervous impulses are in a nerve-fibre. No matter how they have been started, provided their amount is the same, whether they shall produce similar or dissimilar results, depends only on whether they are connected with similar or dissimilar end-organs.

To sum up: Afferent and efferent nerve-fibres differ in no fundamental physiological property; they are simple transmitters, everywhere alike in faculty. We may extend this statement to the subdivisions of each kind, and say that motor, vasomotor and secretory efferent fibres, and tactile, auditory and visual afferent fibres are in all essentials like one another; and that a nervous impulse is alike in every nerve, varying it may be in intensity and in the rate at which others succeed it, in different cases, but the same in kind. Just as all muscles are alike in general physiological properties, and differ in special function according to the parts on which they act, so are all nerve-fibres alike in general physiological properties, and differ in special function only because

they are attached to special things. The special physiology of various nerves will hereafter be considered in connection with the working of various mechanisms in the Body.

The Nature of a Nervous Impulse. Since between sense-organs and sensory centres, and these latter and the muscles, nervous impulses are the only means of communication, it is through them that we arrive at our opinions concerning the external universe and through them that we are able to act upon it; their ultimate nature is therefore a matter of great interest, but one about which we unfortunately know very little. We cannot well imagine it anything but a mode of motion of the molecules of the nerve-fibres, but beyond this hypothesis we cannot go far. In many points the phenomena presented by nerve-fibres as transmitters of disturbances are like the phenomena of wires as transmitters of electricity, and when the phenomena of current electricity were first observed there was a great tendency, explaining one unknown by another, to consider nervous impulses merely as electrical currents. The increase of our knowledge concerning both nerves and electric currents, however, has made such an hypothesis almost, if not quite, untenable. In the first place nerve-fibres are extremely bad conductors of electricity—so bad that it is impossible to suppose them used in the Body for that purpose; and in the second place, merely physical continuity of a nerve-fibre, such as would not interfere with the passage of an electric current, will not suffice for the transmission of a nervous impulse. For instance if a damp string be tied around a nerve, or if it be cut and its two moist ends placed in contact, no nervous impulse will be transmitted across the constricted or divided point although an electrical current would pass readily. An electrical shock may be used like many other stimuli to upset the equilibrium of the nerve-molecules and start a nervous impulse, which then travels along the fibre, but is just as different from the stimulus exciting it as a muscular contraction is from the stimulus which calls it forth.

Careful study of the action-current gives, perhaps, some information regarding the nature of nervous impulses. That local negativity which causes the current begins at the stimulated point of a nerve at the same time as the nervous impulse and travels along the nerve at the same rate. Hence we con-

clude that the new internal molecular arrangement in a nerve-fibre which constitutes its active as compared with its resting state, is one which changes also the electrical properties of the fibre. Now it is found that the negative variation travels along the nerve (in the frog) at the rate of 28 metres (92.00 feet) in a second, and takes .0007 second to pass by a given point : accordingly at any one moment it extends over about 18 mm. (0.720 inch) of the nerve-fibre. Moreover, when first reaching a point it is very feeble, then rises to a maximum, and gradually fades away again. Taking it as an indication of what is going on in the nerve, we may assume that the nervous impulse is a progressive molecular change of a wavelike character, rising from a minimum to a maximum, then gradually ceasing, and about 18 millimetres in wave-length.

A nervous impulse does not appear to exhaust a fibre when transmitted along it. As a ray of light traversing the ether sets up a transient change in it but does not in any way use it up or leave it less fit to transmit a succeeding ray, so it is with the nervous impulse in its transmission. It is true that when a motor nerve attached to a muscle is continuously stimulated the muscular contractions cease after a certain time, though the muscle still responds to electrical stimulation directly applied, and it has been argued that we thus get evidence of the exhaustion of the nerve; but it must be borne in mind that an electrical shock directly applied is undoubtedly a much more powerful stimulus to the muscle than any nervous impulse, and the muscle may have been so fatigued by its previous work as to have become irresponsive to stimulation through its nerve, though still reacting to the grosser excitation. And we have direct evidence that stimulation of a nerve may be continued for a very long time with out causing loss of activity. As an instance, we may take the nerve already mentioned which stops the beat of the heart: when it is stimulated continuously for a few seconds the heart breaks beyond its control and begins to beat again, though the stimulation of the nerve be kept up. This, however, is due to fatigue of the endings of the nerve in the heart, and not of the nerve fibres, as may be proved in this way: the nerve (pneumo-gastric) being carefully exposed in the neck is artificially cooled in one region to below the temperature at which it can conduct a nervous impulse; it is then stimulated at a point nearer the head than the cooled portion: the

resulting impulses being blocked on their way to the heart it goes on beating regularly. After stimulation of the nerve has been continued for several minutes the cooled tract of the nerve is allowed to warm again until it becomes capable of transmitting a nervous impulse; then the heart-beat is found to be promptly stopped or slowed. This shows that if the cardiac endings of the nerve be protected from fatigue, prolonged stimulation of the nerve-trunk does not interfere with its functional capacity: the stimulation still starts nervous impulses in it, which as soon as they can pass on produce their normal effect on the heart. When long-continued sensations become dulled the explanation is no doubt similar: it is the end-organs, central or peripheral, or both, which are exhausted, not the nerve-fibres themselves. It has, however, been observed that when artificial stimulation is long applied to one point on a nerve-trunk that point sometimes becomes unexcitable, though the nerve in general is still quite functional and acts perfectly when the point of application of the stimulus is shifted a little: this is especially the case with gray nerve-fibres and white fibres having a thin medullary sheath.

The very sparse blood-supply of nerve-trunks is in great contrast to the rich supply of those parts of the nervous system containing nerve-cells and to the abundant supply of muscles, and is an evidence that the chemical changes taking place in them during both rest and activity are but small. Seeing that functional activity leads to little or no using up of the conductive substance of a nerve-fibre any more than the transmission of a galvanic current uses up a copper wire, the term *irritable* is not properly applicable to nerve-fibres. Irritability in its physiological sense we have defined as a condition of a living tissue such that a very small extraneous force acting on it may cause it to set free a disproportionately large amount of energy, and in that sense muscle-fibres and nerve-cells are truly irritable, and they both use up their material when at work and are subject to exhaustion. Nerve-fibres are *excitable* and *conductive*, but not really irritable, though on account of their great excitability they are very generally spoken of as irritable.

The Rate of Transmission of a Nervous Impulse. This can be measured in several ways. One of the simplest is a modification of the simple nerve-muscle experiment il-

lustrated in Fig. 62. The muscle M is dissected out with its motor nerve attached, and the stimulus applied to the nerve and not directly to the muscle. First the stimulus is given to the nerve close to the muscle: it is then found that the period of latent excitation, as shown by the greater length of tu, is a very little longer than when the muscle is directly stimulated. Next the stimulus is applied to the nerve, say two inches from the muscle, and it is found that tu is considerabiy longer, the increase in its length being due to the time taken by the nervous impulse in travelling along two inches of nerve. As we know the rate of movement of the surface S, we can readily calculate the amount of the time increase. The rate of travel of the nervous impulse as thus ascertained is almost incomparably slower than that of an electric current, being 28 metres (92.00 feet) per 1″. In the motor nerves of warm-blooded animals the rate of transmission is somewhat faster. Considerable difficulties are met with in making corresponding measurements on afferent nerves, and the rates obtained by different observers differ widely: probably the impulse travels at about the same speed as in the motor nerves of the same animal.

Functions of the Spinal Nerve-Roots. The great majority of the larger nerve-trunks of the Body contain both afferent and efferent nerve-fibres. If one be exposed in its course and divided in a living animal, it will be found that irritating its peripheral stump causes muscular contractions, and pinching its central stump causes signs of sensation, showing that the trunk contained both motor and sensory fibres. If the trunk be followed away from the centre, as it breaks up into smaller and smaller branches, it will be found that these too are mixed until very near their endings, where the very finest terminal branches close to the end-organs, whether muscular fibres, secretory cells, or sensory apparatuses, are only afferent or efferent. If the nerve-trunk be one that arises from the spinal cord and be examined progressively back to its origin, it will still be found mixed, up to the point where its fibres separate to enter either a ventral or a dorsal nerve-root. Each of these latter, however, is *pure*, all the efferent fibres leaving the cord by the ventral or anterior roots, and all the afferent entering it by the posterior or dorsal. This of course could not be learned from examination of the dead nerves, since the best micro-

scope fails to distinguish an afferent from an efferent fibre, but is readily proved by a simple experiment. If an anterior root be cut and its outer end stimulated, the muscles of the parts to which the trunk which it helps to form is distributed will be made to contract, and the skin will be made to sweat also if the root happen to be one that contains secretory fibres for the sweat-glands. On the other hand, if the central end of the root (that part of it attached to the cord) be stimulated no result will follow, showing that the root contains no sensory, reflex, or excito-motor fibres. With the posterior roots the reverse is the case: if one of them be divided and its outer end stimulated, no observed result follows, showing the absence of all efferent fibres; but stimulation of its central end will cause either signs of feeling, or reflex actions, or both. We might compare a spinal nerve-trunk to a rope made up of green and red threads with at one end all the green threads collected into one skein and the red into another, which would represent the roots. At its farthest end we may suppose the rope divided into finer cords, each of these containing both red and green threads, down to the very finest branches consisting of only a few threads, and those all of one kind, either red or green, one representing efferent, the other afferent, fibres.

The Cranial Nerves. Most of these are mixed also, but with one exception (the fifth pair, the small root of which is efferent and the large gangliated one afferent) they do not present distinct motor and sensory roots, like those of the spinal nerves. At their origin from the brain most of them are purely afferent or purely efferent, and the mixed character which their trunks exhibit is due to cross-branches with neighboring nerves, in which afferent and efferent fibres are interchanged. The olfactory, optic, and auditory nerves remain, however, purely afferent in all their course, and others, though not quite pure, contain mainly efferent fibres (as the facial) or mainly afferent (as the glosso-pharyngeal).

The Intercommunication of Nerve-Centres. From the anatomical arrangement of the nervous system it is clear that it forms one continuous whole. No subdivision of it is isolated from the rest, but nerve-trunks proceeding from the centres in one direction bind them to various tissues and, proceeding in another, to other nerve-centres, which in turn are united with other tissues and other centres. Since the

physiological character of a nerve-fibre is its conductivity— its power of propagating a disturbance when once its molecular equilibrium has been upset at any one point—it is obvious that through the nervous system any one part of the Body, supplied with nerves, may react on all other parts (with the exception of such as hairs and nails and cartilages, which are not known to possess nerves) and excite changes in them. Pre-eminently the nervous system forms a uniting anatomical and physiological bond through the agency of which unity and order are produced in the activities of different and distant parts. We may compare it to the Western Union Telegraph, the head office of which in New York would represent the brain and spinal cord, the more important central offices in other large cities the sympathetic ganglia, and the minor offices in country stations the sporadic ganglia; while the telegraph-wires, directly or indirectly uniting all, would correspond to the nerve-trunks. Just as information started along some outlying wire may be transmitted to a central office, and from it to others, and then, according to what happens to it in the centre, be stopped there, or spread in all directions, or in one or two only, so may a nervous disturbance reaching a centre by one nerve-trunk merely excite changes in it or be radiated from it through other trunks more or less widely over the Body and arouse various activities in its other component tissues. In common life the very frequency of this uniting activity of the nervous system is such that we are apt to entirely overlook it. We do not wonder how the sight of pleasant food will make the mouth water and the hand reach out for it; it seems, as we say, "natural," and to need no explanation. But the eye itself can excite no desire, cause the secretion of no saliva, and the movement of no limb. The whole complex result depends on the fact that the eye is united by the optic nerve with the brain, and that again by other nerves with saliva-forming cells, and with muscular fibres of the arm; and through these a change excited by light falling into the eye is enabled to produce changes in far-removed organs, and excite desire, secretion, and movement. In cases of disease this action exerted at a distance is more apt to excite our attention: vomiting is a very common symptom of certain brain diseases, and most people know that a disordered stomach will produce a headache; while the pain consequent

upon the hip-disease of children is usually felt, not at the hip-joint, but at the knee.

The Degeneration of Nerve-Fibres separated from their Centre. A nerve-fibre may in its course be connected with more than one nerve-cell, but one cell always has a special influence in maintaining its normal structure and functional activity. If cut off from this cell the separated portion undergoes degenerative changes, easily recognized in medullated fibres by a breaking up and, later, a disappearance of the medullary sheath. If, for example, the sciatic nerve of a warm-blooded animal be completely cut across, all of the nerve and its branches beyond the point of section will show marked changes in three days or less: the medullary sheath separates into small cuboidal pieces, these in a day or two more round off at their corners and then are gradually absorbed, so that at the end of ten days or a fortnight they have entirely disappeared. Meantime the nuclei of the internodes multiply and the usually sparse protoplasm around them increases, and encroaches upon and causes the absorption of the axis cylinder, so that after some weeks little or no trace of true nervous elements can be found. Some three or four days after making the section the peripheral portion of the nerve ceases to be excitable. If the part of the nerve above the section be examined, its fibres will be found to have undergone no degeneration except close to the place of section, and it remains excitable; pinching it causes pain, and if any muscle branch arising from it be irritated, the muscles contract. If instead of cutting a whole mixed nerve-trunk, such as the sciatic, we divide only a ventral spinal root (as 5, c, Fig. 71), it is found that all the fibres in that part of the root which is cut off from the spinal cord degenerate and become unirritable, and degenerated fibres can be found in the mixed trunk into which the cut root is continued; while the fibres of the part of the root still attached to the cord do not degenerate. The nutritional integrity of the anterior root-fibres depends therefore on anatomical continuity with the spinal cord, and probably with cells there, of the type shown in Fig. 81. On the other hand, if the dorsal root only be cut across, the portion of it attached to the cord degenerates, while that still connected to the spinal ganglion and the fibres beyond the ganglion remain unaltered: the nutritive centres for the dorsal root-fibres are the cells of the corresponding root-ganglion.

After complete section of the nerve-trunk supplying a region of the Body that region is for a time paralyzed, but feeling and the power of movement may return to it. It used to be thought that in such cases the divided nerve-fibres grew together again. Such is not the case: all those parts of the fibres which have been cut off from their centres completely disappear, and when function is restored it is by the formation of new nerve-fibres around outgrowths from the cut ends of those parts of the fibres still united to their centres, whether these be in brain, spinal cord, spinal ganglia, or elsewhere.

Nerves, as we have seen, often give fibres to one another by means of uniting branches, as in various plexuses and elsewhere; and when a nerve-branch may contain fibres derived from some one of two or more original trunks which have communicating branches, it is often of importance to determine in which original trunk its fibres left the brain or spinal cord. In such cases the determination may often be made by dividing one of the possible sources of origin and after a few days examining the branch for degenerated fibres, which are easily recognized by the microscope. If such are found, then they left the centre in the divided trunk; if not, the branch gets no fibres from that trunk. This method of tracking the nerve-fibres of a given original trunk to their final distribution in one or more of many possible branches is known as the *Wallerian method.* Instances of its application will be given in later chapters.

CHAPTER XIV.

THE ANATOMY OF THE HEART AND BLOOD-VESSELS.

General Statement. During life the blood is kept flowing with great rapidity through all parts of the Body (except the few non-vascular tissues already mentioned) in definite paths prescribed for it by the heart and blood-vessels. These paths, which under normal circumstances it never leaves, constitute a continuous set of closed tubes (Fig. 87) beginning at and ending again in the heart, and simple only close to that organ. Elsewhere it is greatly branched, the most numerous and finest branches (*l* and *a*) being the *capillaries*. The heart is essentially a bag with muscular walls, internally divided into four chambers (*d, g, e, f*). Those at one end (*d* and *e*) receive blood from vessels opening into them and known as the *veins*. From there the blood passes on to the remaining chambers (*g* and *f*) which have very powerful walls and, forcibly contracting, drive the blood out into vessels (*m* and *b*) which communicate with them and are known as the *arteries*. The big arteries divide into smaller; these into smaller again (Fig. 88) until the branches become too small to be traced by the unaided eye, and these smallest branches end in the *capillaries*, through which the blood flows and enters the commencements of the *veins ;* and these convey it again to the heart. At certain points in the course of the blood-paths valves are placed, which prevent a back-flow. This alternating reception of blood at one end by the heart and its ejection from the other go on during life steadily about seventy times in a minute, and so keep the liquid constantly in motion.

Fig. 87.—The heart and blood-vessels diagrammatically represented.

The vascular system is completely closed except at two points in the neck where lymph-vessels open into the veins; there some lymph is poured in and mixed directly with the blood. Accordingly everything which leaves the blood must do so by oozing through the walls of the blood-vessels, and everything which enters it must do the same, except matters

R   1   U

Fig. 88.—The arteries of the hand, showing the communications or anastomoses of different arteries and the fine terminal twigs given off from the larger trunks; these twigs end in the capillaries which would only become visible if magnified. *R*, the *radial artery* on which the pulse is usually felt at the wrist; *U*, the ulnar artery

conveyed in by the lymph at the points above mentioned. This interchange through the walls of the vessels takes place only in the capillaries, which form a sort of irrigation system all through the Body. The heart, arteries, and veins are all merely arrangements for keeping the capillaries full and renewing the blood within them. It is in the capillaries alone that the blood does its physiological work.

The Position of the Heart. The heart (*h*, Fig. 1) lies in the chest immediately above the diaphragm and opposite the lower two thirds of the breast-bone. It is conical in form with its *base* or broader end turned upwards and projecting a little on the right of the sternum, while its narrow end or apex, turned downwards, projects to the left of that bone, where it may be felt beating between the cartilages of the fifth and sixth ribs. The position of the organ in the Body is therefore oblique with reference to its long axis. It does not, however, lie on the left side as is so commonly supposed but very nearly in the middle line, with the upper part inclined to the right, and the lower (which may be more easily felt beating—hence the common belief) to the left.

The Membranes of the Heart. The heart does not lie bare in the chest but is surrounded by a loose bag composed of connective tissue and called the *pericardium.* This bag, like the heart, is conical but turned the other way, its broad part being lowest and attached to the upper surface of the diaphragm. Internally it is lined by a smooth *serous membrane* like that lining the abdominal cavity, and a similar layer (the *visceral layer* of the pericardium) covers the outside of the heart itself, adhering closely to it. Each of the serous layers is covered by a stratum of flat cells, and in the space between them is found a small quantity of liquid which moistens the contiguous surfaces, and diminishes the friction which would otherwise occur during the movements of the heart.

Internally the heart is also lined by a fibrous membrane, covered with a single layer of flattened cells, and called the *endocardium.* Between the endocardium and the visceral layer of the pericardium the bulk of the wall of the heart lies and is made up mainly of striped muscular tissue (*myocardium*) differing from that of the skeletal muscles; but connective tissues, blood-vessels, nerve-cells, and nerve-fibres are also abundant in it.

Note.—Sometimes the pericardium becomes inflamed, this affection being known as pericarditis. It is extremely apt to occur in acute rheumatism, and great care should be taken never, even for a moment, except under medical advice, to expose a patient to cold during that disease, since any chill is then especially apt to set up pericarditis. In the earlier stages of pericardiac inflammation the rubbing surfaces on

the outside of the heart and the inside of the pericardium become roughened, and their friction produces a sound which can be recognized through the stethoscope. In later stages great quantities of liquid may accumulate in the pericardium so as to seriously impede the heart's beat.

The Cavities of the Heart. On opening the heart (see diagram Fig. 89) it is found to be subdivided by a longi-

Fig. 89.—Diagram representing a section through the heart from base to apex.

tudinal partition or *septum* into completely separated right and left halves, the partition running from about the middle of the base to a point a little on the right of the apex. Each of the chambers on the sides of the septum is again incompletely divided transversely, into a thinner basal portion into which veins open, known as the *auricle*, and a thicker apical portion from which arteries arise, called the *ventricle*. The heart thus consists of a right auricle and ventricle and a left auricle and ventricle, each auricle communicating by an *auriculo-ventricular orifice* with the ventricle on its own side, and there is no direct communication whatever through the septum between the opposite sides of the heart. To get from one side to the other the blood must leave the heart and pass through a set of capillaries, as may readily be seen by tracing the course of the vessels in Fig. 87.

The Heart as seen from its Exterior. When the heart is viewed from the side turned towards the sternum (Fig. 90) the two auricles, *Atd* and *As*, are seen to be separated by a deep groove from the ventricles, *Vd* and *Vs*. A more shallow furrow runs between the ventricles and indicates the position of the internal longitudinal septum. On the dorsal aspect of the heart (Fig. 91) similar furrows may be noted, and on one or other of the two figures the great vessels opening into the cavities of the heart may be seen. The *pulmonary artery, P,* arises from the right ventricle, and very soon divides into the right and left pulmonary arteries, *Pd* and *Ps*, which break up into smaller branches and enter

the corresponding lungs. Opening into the right auricle are two great veins (see also Fig. 89), *cs* and *ci*, known respectively as the *upper* and *lower venæ cavæ*, or "hollow" veins; so called by the older anatomists because they are frequently found empty after death. Into the back of the right auricle opens also another vein, *Vc*, called the *coronary*

Ade   C⁸   Sd   ⟋A

v$

si
ar
lei
in——————————————————————————————————————— tery;
P, main trunk of the pulmonary artery, and *Pd* and *Ps*, its branches to the right and left lungs; *cs*, superior vena cava; *Ade* and *Asi*, the right and left innominate veins; *pd* and *ps*, the right and left pulmonary-veins; *crd* and *crs*, the right and left coronary arteries.

vein or *sinus*, which brings back blood that has circulated in the walls of the heart itself. Springing from the left ventricle, and appearing from beneath the pulmonary artery when the heart is looked at from the ventral side, is a great artery, the *aorta*, *Aa*. It forms an arch over the base of the heart and then runs down behind it at the back of the chest. From the convexity of the arch of the aorta several great

branches are given off, *Ssi, Cs, Ab;* but before that, close to the heart, the aorta gives off two *coronary arteries*, branches of which are seen at *crd* and *crs* lying in the groove over the partition between the ventricles, and which carry to the substance of the organ that blood which comes back through the

Fig. 91.—The heart viewed from its dorsal aspect. *Afd*, right auricle: *ci*, inferior vena cava; *Vc*, coronary vein. The remaining letters of reference have the same signification as in Fig 90.

coronary sinus. Into the left auricle open two right and two left *pulmonary veins, ps* and *pd*, which are formed by the union of smaller veins proceeding from the lungs.

In the diagram Fig. 89 from which the branches of the great vessels near the heart have been omitted for the sake of clearness, the connection of the various vessels with the

chambers of the heart can be better seen. Opening into the right auricle are the superior and inferior venæ cavæ (*cs* and *ci*) and proceeding from the right ventricle the *pulmonary artery, P.* Opening into the left auricle are the right and left pulmonary veins (*pd* and *ps*) and springing from the left ventricle the aorta, *A.*

The Interior of the Heart. The communication of each auricle with its ventricle is also represented in the diagram Fig. 89, and the valves which are present at those points and at the origin of the pulmonary artery and that of the aorta. Internally the auricles are for the most part smooth, but from each a hollow pouch, the *auricular appendage*, projects over the base of the corresponding ventricle as seen at *Adx* and *As* in Figs. 90 and 91. These pouches have somewhat the shape of a dog's ear and have given their name to the whole auricle. Their interior is roughened by muscular elevations, covered by endocardium, known as the fleshy columns (*columnæ carnæ*). On the inside of the ventricles (Fig. 92) similar fleshy columns are very prominent.

The Auriculo-Ventricular Valves. These are known as *right* and *left*, or as the *tricuspid* and *mitral valves* respectively. The mitral valve (Fig. 92) consists of two flaps of the endocardium fixed by their bases to the margins of the auriculo-ventricular aperture and with their edges hanging down into the ventricle when the heart is empty. These unattached edges are not however free, but have fixed to them a number of stout connective-tissue cords, the *cordæ tendineæ*, which are fixed below to muscular elevations, the *papillary muscles, Mpm* and *Mpl*, on the interior of the ventricle. The cords are long enough to let the valve flaps rise into a horizontal position and so close the opening between auricle and ventricle which lies between them, and passes up behind the opened aorta, *Sp*, represented in the figure. The *tricuspid valve* is like the mitral, but with three flaps instead of two.

Semilunar Valves. These are six in number: three at the mouth of the aorta, Fig. 92, and three, quite like them, at the mouth of the pulmonary artery. Each is a strong crescentic pouch fixed by its more curved border, and with its free edge turned away from the heart. When the valves are in action these free edges meet across the vessel and prevent blood from flowing back into the ventricle. In the middle of the free border of each valve is a little cartilagi-

nous nodule, the *corpus Arantii*, and on each side of this the edge of the valve is very thin and when it meets its neighbor turns up against it and so secures the closure.

The Arterial System. All the arteries of the Body arise either directly or indirectly from the aorta or pulmonary artery, and the great majority of them from the former vessel.

Sp

mpm

Fig. 98.—The left ventricle and the commencement of the aorta laid open. *Mpm, Mpl,* the papillary muscles. From their upper ends are seen the *cordæ tendíneæ* proceeding to the edges of the flaps of the mitral valve. The opening into the auricle lies between these flaps. At the beginning of the aorta are seen its three pouch-like semilunar valves.

The pulmonary artery only carries blood to the lungs, to undergo exchanges with the air in them after it has circulated through the Body generally.

After making its arch the aorta continues back through the chest, giving off many branches on its way. Piercing the

diaphragm it enters the abdomen and after supplying the parts in and around that cavity with branches, it ends opposite the last lumbar vertebra by dividing into the *right* and *left common iliac* arteries, which carry blood to the lower limbs. We have then to consider the branches of the arch of the aorta, and those of the *descending aorta,* which latter is for convenience described by anatomists as consisting of the *thoracic aorta,* extending from the end of the arch to the diaphragm, and the *abdominal aorta,* extending from the diaphragm to the final subdivision of the vessel.

Branches of the Arch of the Aorta. From this arise first the *coronary arteries* (*crd* and *crs,* Figs. 90 and 91) which spring close to the heart, just above two of the pouches of the semilunar valve, and carry blood into the substance of that organ. The remaining branches of the arch are three in number, and all arise from its convexity. The first is the *innominate artery* (*Ab,* Fig. 90), which is very short, immediately breaking up into the *right subclavian artery,* and the *right common carotid.* Then comes the *left common carotid, Cs,* and finally the *left subclavian, Ssi.*

Each *subclavian artery* runs out to the arm on its own side and after giving off a *vertebral artery* (which runs up the neck to the head in the vertebral canal of the transverse processes of the cervical vertebræ), crosses the arm-pit and takes there the name of the *axillary artery.* This continues down the arm as the *brachial artery,* which, giving off branches on its way, runs to the front of the arm, and just below the elbow-joint divides into the *radial* and *ulnar arteries,* the lower ends of which are seen at *R* and *U* in Fig. 88. These supply the forearm and end in the hand by uniting to form an arch, from which branches are given off to the fingers.

The *common carotid arteries* pass out of the chest into the neck, along which they ascend on the sides of the windpipe. Opposite the angle of the lower jaw each divides into an *internal* and *external carotid artery,* right or left as the case may be. The external ends mainly in branches for the face, scalp, and salivary glands, one great subdivision of it with a tortuous course, the *temporal artery,* being often seen in thin persons beating on the side of the brow. The internal carotid artery enters the skull through an aperture in its base and supplies the brain, which it will be remembered also gets blood through the vertebral arteries.

Branches of the Thoracic Aorta. These are numerous but small. Some, the *intercostal arteries*, run out between the ribs and supply the chest-walls; others, the *bronchial arteries*, carry blood to the lungs for their nourishment, that carried to them by the pulmonary arteries being brought there for another purpose; and a few other small branches are given to other neighboring parts.

Branches of the Abdominal Aorta. These are both large and numerous, supplying not only the wall of the posterior part of the trunk, but the important organs in the abdominal cavity. The larger are: the *cœliac axis* which supplies stomach, spleen, liver, and pancreas; the *superior mesenteric artery*, which supplies a great part of the intestine; the *renal arteries*, one for each kidney; and finally the *inferior mesenteric artery*, which supplies the rest of the intestine. Besides these the abdominal aorta gives off very many smaller branches.

Arteries of the Lower Limbs. Each common iliac divides into an *internal* and *external iliac artery*. The former mainly ends in branches to parts lying in the pelvis, but the latter passes into the thighs and there takes the name of the *femoral artery*. At first this lies on the ventral aspect of the limb, but lower down passes to the back of the femur, and above the knee-joint (where it is called the *popliteal artery*) divides into the *anterior* and *posterior tibial arteries*, which supply the leg and foot.

The Capillaries. As the arteries are followed from the heart, their branches become smaller and smaller, and finally cannot be traced without the aid of a microscope. Ultimately they pass into the *capillaries*, the walls of which are simpler than those of the arteries, and which form very close networks in nearly all parts of the Body; their immense number compensating for their smaller size. The average diameter of a capillary vessel is .016 mm. ($\frac{1}{1800}$ inch) so that only two or three blood-corpuscles can pass through it abreast, and in many parts they are so close that a pin's point could not be inserted between two of them. It is while flowing in these delicate tubes that the blood does its nutritive work, the arteries being merely supply-tubes for the capillaries.

The Veins. The first veins arise from the capillary networks in various organs, and like the last arteries are very small. They soon increase in size by union, and so form

larger and larger trunks. These in many places lie near or alongside the main artery of the part, but there are many more large veins just beneath the skin than there are large arteries. This is especially the case in the limbs, the main veins of which are superficial, and can in many persons be seen as faint blue marks through the skin. Fig. 94 represents the arm at the front of the elbow joint after the skin and subcutaneous areolar tissue and fat have been removed.

FIG. 93.—A small portion of the capillary network as seen in the frog's web when magnified about 25 diameters. *a*, a small artery feeding the capillaries; *v, v,* small veins carrying blood back from the latter.

The brachial artery, *B*, colored red, is seen lying tolerably deep, and accompanied by two small veins (*venæ comites*) which communicate by cross-branches. The great *median nerve*, 1, a branch of the brachial plexus which supplies several muscles of the forearm and hand, the skin over a great part of the palm and the three inner fingers, is seen alongside the artery. The larger veins of the part are seen

to form a more superficial network, joined here and there, as for instance at *, by branches from deeper parts. Several small nerve-branches which supply the skin (2, 3, 4) are seen among these veins. It is from the vessel, *cep*, called the

Fig. 94.—The superficial veins in front of the elbow-joint. *B'*, tendon of *biceps* muscle; *Bi, brachialis internus* muscle; *Pt, pronator teres* muscle; 1, median nerve; 2, 3, 4, nerve-branches to the skin; *B*, brachial artery, with its small accompanying veins; *cep,* cephalic vein; *bas,* basilic vein; *m',* median vein, *, junction of a deep-lying vein with the cephalic.

cephalic vein, just above the point where it crosses the median nerve, that surgeons usually bleed a patient.

A great part of the blood of the lower limb is brought back by the *long saphenous vein,* which can be seen in thin persons running from the inner side of the ankle to the top of the

thigh. All the blood which leaves the heart by the aorta, except that flowing through the coronary arteries, is finally collected into the *superior* and *inferior venæ cavæ* (*cs* and *ci*, Figs. 90 and 91), and poured into the right auricle. The *jugular veins* which run down the neck, carrying back the blood which went out along the carotid arteries, unite below with the arm-vein (*subclavian*) to form on each side an *innominate vein* (*Asi* and *Ade*, Fig. 90) and the innominates unite to form the superior cava. The coronary-artery blood after flowing through the capillaries of the heart itself also returns to this auricle by the coronary veins and sinus.

The Pulmonary Circulation. Through this the blood gets back to the left side of the heart and so into the aorta again. The pulmonary artery, dividing into branches for each lung, ends in the capillaries of those organs. From these it is collected by the pulmonary veins, which carry it back to the left auricle, whence it passes to the left ventricle to recommence its flow through the Body generally.

The Course of the Blood. From what has been said it is clear that the movement of the blood is a *circulation*. Starting from any one chamber of the heart it will in time return to it; but to do this it must pass through at least two sets of capillaries; one of these is connected with the aorta and the other with the pulmonary artery, and in its circuit the blood returns to the heart twice. Leaving the left side it returns to the right, and leaving the right it returns to the left: and there is no road for it from one side of the heart to the other except through a capillary network. Moreover, it always leaves from a ventricle through an artery, and returns to an auricle through a vein.

There is then really only one circulation; but it is not uncommon to speak of two, the flow from the left side of the heart to the right, through the Body generally, being called the *systemic circulation*, and from the right to the left, through the lungs, the *pulmonary circulation*. But since after completing either of these alone the blood is not back at the point from which it started, but is separated from it by the septum of the heart, neither is a "circulation" in the proper sense of the word.

The Portal Circulation. A certain portion of the blood which leaves the left ventricle of the heart through the aorta has to pass through three sets of capillaries before it can again

return there. This is the portion which goes through the stomach, spleen, pancreas, and intestines. After traversing the capillaries of those organs it is collected into the *portal vein* which enters the liver, and breaking up in it into finer and finer branches like an artery, ends in the capillaries of that organ, forming the second set which this blood passes through on its course. From these it is collected by the *hepatic veins,* which pour it into the inferior vena cava, which carries it to the right auricle, so that it has still to pass through the pulmonary capillaries to get back to the left side of the heart. The portal vein is the only one in the human Body which like an artery feeds a capillary network, and the flow from the stomach and intestines through the liver to the vena cava is often spoken of as the *portal circulation.*

Diagram of the Circulation. Since the two halves of the heart are actually completely separated from one another by an impervious partition, although placed in proximity in the Body, we may conveniently represent the course of the blood as in the accompanying diagram (Fig. 95), in which the right and left halves of the heart are represented at different points in the vascular system. Such an arrangement makes it clear that the heart is really two pumps working side by side, each engaged in forcing the blood to the other. Starting from the left auricle, *la,* and following the flow, we trace it through the left ventricle and along the branches of the aorta into the systemic capillaries, *sc;* from thence it passes back through the systemic veins, *vc.* Reaching the right auricle, *ra,* it is sent into the right ventricle, *rv,* and thence through the pulmonary artery, *pa,* to the lung capillaries, *pc,* from which the pulmonary veins, *pv,* carry it to the left auricle, which drives it into the left ventricle, *lv,* and this again into the aorta.

Fig. 95.—Diagram of the blood vascular system, showing that it forms a single closed circuit with two pumps in it, consisting of the right and left halves of the heart, which are represented separate in the diagram. *ra* and *rv,* right auricle and ventricle; *la* and *lv,* left auricle and ventricle; *ao,* aorta; *sc,* systemic capillaries; *vc,* venæ cavæ; *pa,* pulmonary artery; *pc,* pulmonary capillaries; *pv,* pulmonary veins.

Arterial and Venous Blood. The blood when flowing in the pulmonary capillaries gives up carbon dioxide to the air and receives oxygen from it; and since its coloring matter (hæmoglobin) forms a scarlet compound with oxygen, it flows to the left auricle through the pulmonary veins of a bright red color. This color it maintains until it reaches the systemic capillaries, but in these it loses much oxygen to the surrounding tissues and gains much carbon dioxide from them. But the blood coloring-matter which has lost its oxygen has a dark purple color, and since this unoxidized or "reduced" hæmoglobin is now in excess, the blood returns to the heart by the venæ cavæ of a dark purple-red color. This hue it keeps until it reaches the lungs, when the reduced hæmoglobin becomes again oxidized. The bright red blood, rich in oxygen and poor in carbon dioxide, is known as "arterial blood" and the dark red as "venous blood:" and it must be borne in mind that the terms have this peculiar technical meaning, and that the pulmonary *veins* contain *arterial* blood, and the pulmonary *arteries, venous* blood; the change from arterial to venous taking place in the systemic capillaries, and from venous to arterial in the pulmonary capillaries. The chambers of the heart and the great vessels containing arterial blood are shaded red in Figs. 90 and 91.

The Structure of the Arteries. A large artery can by careful dissection be separated into three coats: an *internal*, a *middle*, and an *outer*. The internal coat tears readily across the long axis of the artery and consists of an inner lining of flattened nucleated cells, enveloped by a variable number of layers composed of membranes or networks of elastic tissue. The middle coat is made up of alternating layers of elastic fibres and plain muscular tissue; the former running for the most part longitudinally and the latter across the long axis of the vessel. The outer coat is the toughest and strongest because it is mainly made up of white fibrous connective tissue; it contains a considerable amount of elastic tissue also, and gradually shades off into a loose areolar tissue which forms the *sheath* of the artery, or the *tunica adventitia,* and packs it between surrounding parts. The smaller arteries have all the elastic elements less developed. The internal coat is consequently thinner, and the middle coat is made up mainly of involuntary muscular fibres. As a result the large arteries are highly elastic, the aorta being physically much like a piece of india-rubber tubing, while the smaller arte-

ries are highly contractile, in the physiological sense of the word.

Structure of the Capillaries. In the smaller arteries the outer and middle coats gradually disappear, and the elastic layers of the inner coat also go. Finally, in the capillaries the lining epithelium alone is left, with a more or less developed layer of connective-tissue corpuscles around it, representing the remnant of the tunica adventitia. These vessels are thus extremely well adapted to allow of filtration or diffusion taking place through their thin walls.

Structure of the Veins. In these the same three primary coats as in the arteries are found; the inner and middle coats are less developed, while the outer one remains thick, and is made up almost entirely of white fibrous tissue. Hence the venous walls are much thinner than those of the corresponding arteries, and the veins collapse when empty while the stouter arteries remain open. But the toughness of their outer coats gives the veins great strength.

Except the pulmonary artery and the aorta, which possess the semilunar valves at their cardiac orifices, the arteries possess no valves. Many veins on the contrary have such, formed by semilunar pouches of the inner coat, attached by one margin and having the edge turned towards the heart free. These valves, sometimes single, oftener in pairs, and rarely three at one level, permit blood to flow only towards the heart, for a current in that direction (as in the upper diagram, Fig. 96) presses the valve close against the side of the vessel and meets with no obstruction from it. Should any back-flow be attempted, however, the current closes up the valve and bars its own passage as indicated in the lower figure. These valves are most numerous in superficial veins and those of muscular parts. They are absent in the venæ cavæ and the portal and pulmonary veins. Usually the vein is a little dilated opposite a valve, and hence in parts where the

Fig. 96.—Diagram to illustrate the mode of action of the valves of the veins. *C*, the capillary, and *H*, the heart end of the vessel.
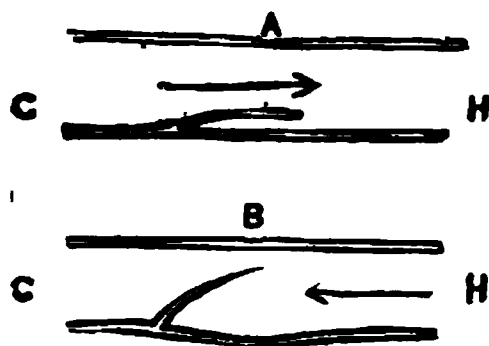
valves are numerous gets a knotted look. On compressing the forearm so as to stop the flow in its subcutaneous veins and cause their dilatation, the points at which valves are placed can be recognized by their swollen appearance. They are most frequently situated where two veins communicate.

CHAPTER XV.

THE WORKING OF THE HEART AND BLOOD-VESSELS.

The Beat of the Heart. It is possible with some little skill and care to open the chest of a living narcotized animal, such as a rabbit, and see its heart at work, alternately contracting and diminishing the cavities within it, and relaxing and expanding them. It is then observed that each beat commences at the mouths of the great veins; from there runs over the rest of the auricles, and then over the ventricles; the auricles commencing to dilate the moment the ventricles commence to contract. Having finished their contraction the ventricles also commence to dilate, and so for some time neither they nor the auricles are contracting, but the whole heart is expanding. The contraction of any part of the heart is known as its *systole* and the relaxation as its *diastole,* and since the two sides of the heart work synchronously, the auricles together and the ventricles together, we may describe a whole "cardiac period" or "heart-beat" as made up successively of *auricular systole, ventricular systole,* and *pause.* This cycle is repeated about seventy times a minute; and if the whole time occupied by it be subdivided into 100 parts, about 9 of these will be occupied by the auricular systole, about 30 by the ventricular systole, and 61 by the pause: during more than half of life, therefore, the muscle-fibres of the heart are at rest. In the *pause* the heart if taken between the finger and thumb feels soft and flabby, but during the systole it (especially its ventricular portion) becomes hard and rigid.

Change of Form of the Heart. During its systole the heart becomes shorter and rounder, mainly from a change in the shape of the ventricles. A cross-section of the heart at the base of these latter during diastole would be elliptical in outline, with its long diameter from right to left; during the systole it is more circular, the long axis of the ellipse becoming shortened, while the dorso-ventral diameter remains little

altered. At the same time the length of the ventricles is lessened, the apex of the heart approaching the base and becoming blunter and rounder.

The Cardiac Impulse. The human heart lies with its apex touching the chest-wall between the fifth and sixth ribs on the left side of the breast-bone. At every beat a sort of tap, known as the "cardiac impulse" or "apex beat," may be felt by the finger at that point. There is, however, no actual "tapping," since the heart's apex never leaves the chest-wall. During the diastole the soft ventricles yield to the chest-wall where they touch it, but during the systole they become hard and tense and push it out a little between the ribs, and so cause the apex beat. Since the heart becomes shorter during the ventricular systole, it might be supposed that at that time the apex would move up a little in the chest. This, however, is not the case, the ascent of the apex towards the base of the ventricles being compensated for by a movement of the whole heart in the opposite direction. If water be pumped into an elastic tube, already moderately full, the tube will be distended not only transversely but longitudinally. This is what happens in the aorta: when the left ventricle contracts and pumps blood forcibly into it, the elastic artery is elongated as well as widened, and the lengthening of that limb of its arch attached to the heart pushes the latter down towards the diaphragm, and compensates for the upward movement of the apex due to the shortening of the ventricles. Hence if the exposed living heart be watched it appears as if during the systole the base of the heart moved towards the tip, rather than the reverse.

Events occurring within the Heart during a Cardiac Period. Let us commence at the end of the ventricular systole. At this moment the semilunar valves at the orifices of the aorta and the pulmonary artery are closed, so that no blood can flow back from those vessels. The whole heart, however, is soft and distensible and yields readily to blood flowing into it from the pulmonary veins and the venæ cavæ; this passes on through the open mitral and tricuspid valves and fills up the dilating ventricles, as well as the auricles. As the ventricles fill, back currents are set up along their walls and these carry up the flaps of the valves so that by the end of the pause they are nearly closed. At this moment the auricles contract, and since this contraction commences at and

narrows the mouths of the veins opening into them, and at the same time the blood in those vessels opposes some resistance to a back-flow into them, while the still flabby and dilating ventricles oppose much less resistance, the general result is that the contracting auricles send blood into the ventricles, and not back into the veins. At the same time the increased direct current into the ventricles produces a greater back current on the sides, which, when the auricles cease their contraction and the filled ventricles become tense and press on the blood inside them, completely closes the auriculo-ventricular valves. That this increased filling of the ventricles, due to auricular contractions, will close the valves may be seen easily in a sheep's heart. If the auricles be carefully cut away from this so as to expose the mitral and tricuspid valves, and water be then poured from a little height into the ventricles, it will be seen that as these cavities are filled the valve-flaps are floated up and close the orifices.

The auricular contraction now ceases and the ventricular commences. The blood in each ventricle is imprisoned between the auriculo-ventricular valves behind and the semilunar valves in front. The former cannot yield on account of the cordæ tendineæ fixed to their edges: the semilunar valves, on the other hand, can open outwards from the ventricle and let the blood pass on, but they are kept tightly shut by the pressure of the blood on their other sides, just as the lock-gates of a canal are by the pressure of the water on them. In order to open the canal-gates water is let in or out of the lock until it stands at the same level on each side of them; but of course they might be forced open without this by applying sufficient power to overcome the higher water pressure on one side. It is in this latter way that the semilunar valves are opened. The contracting ventricle tightens its grip on the blood inside it and becomes rigid to the touch. As it squeezes harder and harder, at last the pressure on the blood within it becomes greater than the pressure exerted on the other side of the valves by the blood in the arteries, the flaps are forced open and the blood begins to pass out: the ventricle continues its contraction until it has obliterated its cavity and completely emptied itself; this total emptying appears, at least, to occur in the normally beating heart, but in some pathological conditions and under the influence of certain drugs the emptying of the ventricles is incomplete. After

the systole the ventricle commences to relax and blood immediately to flow back towards it from the highly stretched arteries. This return current, however, catches the pockets of the semilunar valves, drives them back and closes the valve so as to form an impassable barrier; and so the blood which has been forced out of either ventricle cannot flow directly back into it.

Use of the Papillary Muscles. In order that the contracting ventricles may not force blood back into the auricles it is essential that the flaps of the mitral and tricuspid valves be maintained in position across the openings which they close, and be not pushed back into the auricles. At the commencement of the ventricular systole this is provided for by the cordæ tendineæ, which are of such a length as to keep the edges of the flaps in apposition, a position which is farther secured by the fact that each set of cordæ tendineæ (Fig. 92) radiating from a point in the ventricle, is not attached around the edges of one flap but on the contiguous' edges of two flaps, and so tends to pull them together. But as the contracting ventricles shorten, the cordæ tendineæ, if directly fixed to their interior, would be slackened and the valve-flaps pushed up into the auricle. The little papillary muscles prevent this. Shortening as the ventricular systole proceeds, they keep the cordæ taut and the valves closed.

The mechanism is indeed even better working than this. The area of the valve-flaps is greater than is sufficient to stretch across the auriculo-ventricular orifice, so that when their edges are in apposition they form a cone projecting into the ventricle. Towards the ends of the systole the papillary muscles pull this cone down into the ventricular cavity so as to practically obliterate it and force out from it nearly every drop of blood.

Sounds of the Heart. If the ear be placed on the chest over the region of the heart during life, two distinguishable sounds will be heard during each cardiac cycle. They are known respectively as the first and second sounds of the heart. The first is of lower pitch and lasts longer than the second and sharper sound: vocally their character may be tolerably imitated by the words *lubb, dŭp*. The cause of the second sound is the closure, or, as one might say, the "clicking up," of the semilunar valves, since it occurs at the moment of their closure and ceases if they be hooked back in

a living animal. The origin of the first sound is still uncertain: it takes place during the ventricular systole and is probably due to vibrations of the tense ventricular wall at that time. It is not due, at least not entirely, to the auriculo-ventricular valves, since it may still be heard in a beating heart empty of blood, and in which there could be no closure or tension of those valves. In various forms of heart disease these sounds are modified or cloaked by additional "murmurs" which arise when the cardiac orifices are roughened or narrowed or dilated, or the valves inefficient. By paying attention to the character of the new sound then heard, the exact period in the cardiac cycle at which it occurs, and the region of the chest-wall at which it is heard most distinctly, the physician can often get important information as to its cause.

Diagram of the Events of a Cardiac Cycle. In the following table the phenomena of the heart's beat are represented with reference to the changes of form which are seen on an exposed working heart. Events in the same vertical column occur simultaneously; on the same horizontal line, from left to right, successively.

	Auricular Systole.	Commencement of Ventricular Systole.	Ventricular Systole.	Cessation of Ventricular Systole.	Pause.
Auricles.........	Contracting and emptying.	Dilating and filling.	Dilating and filling.	Dilating and filling.	Dilating and filling.
Ventricles........	Dilating and filling.	Contracting.	Contracting and emptying.	Dilating.	Dilating and filling.
Impulse	....	Apex beat.	....	....	... .
Auriculo-ventricular valves	Closing.	Closed.	Closed.	Opening.	Open.
Semilunar valves	Closed.	Closed.	Open.	Closing.	Closed.
Sounds..........	....	First sound.	....	Second sound.	....

Function of the Auricles. The ventricles have to do the work of pumping the blood through the blood-vessels. Accordingly their walls are far thicker and more muscular than those of the auricles; and the left ventricle, which has to force the blood over the Body generally, is stouter than the right, which has only to send blood around the comparatively short pulmonary circuit. The circulation of the blood is in fact maintained by the ventricles, and we have to inquire what is the use of the auricles. Not unfrequently the heart's

action is described as if the auricles first filled with blood and then contracted and filled the ventricles; and then the latter contracted and drove the blood into the arteries. From the account given above, however, it will be seen that the events are not accurately so represented, but that during all the pause blood flows on through the auricles into the ventricles, which latter are already nearly full when the auricles contract; this contraction merely completing their filling and finishing the closure of the auriculo-ventricular valves. The real use of the auricles is to afford a reservoir into which the veins may empty while the comparatively long-lasting ventricular contraction is taking place: they also largely control the amount of work done by the heart.

If the heart consisted of the ventricles only, with valves at the points of entry and exit of the blood, the circulation could be maintained. During diastole the ventricle would fill from the veins, and during systole empty into the arteries. But in order to accomplish this, during the systole the valves at the point of entry must be closed, or the ventricle would empty itself into the veins as well as into the arteries; and this closure would necessitate a great loss of time which might be utilized for feeding the pump. This is avoided by the auricles, which are really reservoirs at the end of the venous system, collecting blood when the ventricular pump is at work. When the ventricles relax, the blood entering the auricles flows on into them: but previously, during the $\frac{80}{100}$ of the cardiac cycle occupied by the ventricular systole, the auricles have accumulated blood, and when they at last contract they send on into the ventricles this accumulation. Even were the flow from the veins stopped during the auricular contraction this would be of comparatively little consequence, since that event occupies so brief a time. But, although no doubt somewhat lessened, the emptying of the veins into the heart does not seem to be, in health, stopped while the auricle is contracting. For at that moment the ventricle is relaxing and receives the blood from the auricles under a less pressure than it enters the latter from the veins. The heart in fact consists of a couple of " feed-pumps "—the auricles—and a couple of " force-pumps "—the ventricles; and so wonderfully perfect is the mechanism that the supply to the feed-pumps is never stopped. The auricles are never empty, being supplied all the time of their contraction, which

is never so great as to obliterate their cavities; while the ventricles contain no blood at the end of their systole.

The auricles also govern to a certain extent the amount of work done by the ventricles. These latter contract with more than sufficient force to completely drive out all the blood contained in them. If the auricles contract more powerfully and empty themselves more completely at any given time, the ventricles will contain more blood at the commencement of their systole, and will have pumped out more at its end. Now, as we shall see in Chapter XVIII, the contraction of the auricles is under the control of the nervous system, and through the auricles the whole work of the heart. In fact the ventricles represent the brute force concerned in maintaining the circulation, while the auricles are part of a highly-developed co-ordinating mechanism, by which the rate of the blood-flow is governed according to the needs of the whole Body at the time.

The Work Done by the Heart. This can be calculated with approximate correctness. At each systole each ventricle sends out the same quantity of blood—about 180 grams (6.3 ounces); the pressure exerted by the blood in the aorta against the semilunar valves, and which the ventricle has to overcome, is about that which would be exerted on the same surface by a column of mercury 200 millimeters (8 inches) high. The left ventricle therefore drives out, seventy times in a minute, 180 grams (6.3 ounces) of blood against this pressure. Since the specific gravity of mercury is 12.5 and that of blood may for practical purposes be taken as 1, the work of each stroke of the ventricle is equivalent to raising 180 grams (6.3 ounces) of blood $200 \times 12.5 = 2500$ millim. (8.2 feet); or one gram 450 meters (one ounce 51.66 feet); or one kilogram 0.45 meter (one lb. 3.23 feet). Work is measured by the amount of energy needed to raise a definite weight a given distance against gravity at the earth's surface, the unit, called a *kilogrammeter*, being either that necessary to raise one kilogram one meter, or, called a *foot-pound*, that necessary to raise one pound one foot. Expressed thus the work of the left ventricle in one minute, when the heart's rate is seventy strokes in that time, is $0.45 \times 70 = 31\ 50$ kilogrammeters ($3.23 \times 70 = 226.1$ foot-pounds); in one hour it is $31.50 \times 60 = 1890$ kilogrammeters ($226.1 \times 60 = 13,566$ foot-pounds); and in twenty-four hours $1890 \times 24 = 45,360$

kilogrammeters (325,584 foot-pounds). The pressure in the pulmonary artery against which the right ventricle works is about ⅓ of that in the aorta; hence this ventricle in twenty-four hours will do one third as much work as the left, or 15,120 kilogrammeters (108,528 foot-pounds), and adding this to the amount done by the left, we get as the total work of the ventricles in a day the immense amount of 60,480 kilogrammeters (434,112 foot-pounds). If a man weighing 75 kilograms (165 lbs.) climbed up a mountain 806 meters (2644 feet) high his skeletal muscles would probably be greatly fatigued at the end of the ascent, and yet in lifting his Body that height they would only have performed the amount of work that the ventricles of the heart do daily without fatigue.

The Flow of the Blood Outside the Heart. The blood leaves the heart intermittently and not in a regular stream, a quantity being forced out at each systole of the ventricles: before it reaches the capillaries, however, this rhythmic movement is transformed into a steady flow, as may readily be seen by examining under the microscope thin transparent parts of various animals, as the web of a frog's foot, a mouse's ear, or the tail of a small fish. In consequence of the steadiness with which the capillaries supply the veins the flow in these is also unaffected, directly, by each beat of the heart; if a vein be cut the blood wells out uniformly, while a cut artery spurts out not only with much greater force, but in jets which are much more powerful at regular intervals corresponding with the systoles of the ventricles.

The Circulation of the Blood as Seen in the Frog's Web. There is no more fascinating or instructive phenomenon than the circulation of the blood as seen with the microscope in the thin membrane between the toes of a frog's hind limb. Upon focusing beneath the epidermis a network of minute arteries, veins, and capillaries, with the blood flowing through them, comes into view (Fig. 91). The arteries, *a*, are readily recognized by the fact that the flow in them is fastest and from larger to smaller branches. The latter are seen ending in capillaries, which form networks, the channels of which are all nearly equal in size. While in the veins arising from the capillaries the flow is from smaller to larger trunks, and slower than in the arteries, but faster than in the capillaries.

The reason of the slower flow of the capillaries is that their united area is considerably greater than that of the arteries supplying them, so that the same quantity of blood flowing through them in a given time has a wider channel to flow in and moves more slowly. The area of the veins is smaller than that of the capillaries but greater than that of the arteries, and hence the rate of movement in them is also intermediate. Almost always when an artery divides, the area of its branches is greater than that of the main trunk, and so the arterial current becomes slower and slower from the heart onwards. In the veins, on the other hand, the area of a trunk formed by the union of two or more branches is less than that of the branches together, and the flow becomes quicker and quicker towards the heart. But even at the heart the united cross-sections of the veins entering the auricles are greater than those of the arteries leaving the ventricles, so that, since as much blood returns to the heart in a given time as leaves it, the rate of the current in the pulmonary veins and the venæ cavæ is less than in the pulmonary artery and aorta. We may represent the vascular system as a double cone, widening from the ventricles to the capillaries and narrowing from the latter to the auricles. Just as water forced in at a narrow end of this would flow quickest there and slowest at the widest part, so the blood flows quickest in the aorta and slowest in the capillaries, which taken together form a much wider channel.

The Axial Current and the Inert Layer. If a small artery in the frog's web be closely examined it will be seen that the rate of flow is not the same in all parts of it. In the centre is a very rapid current carrying along all the red corpuscles and known as the *axial stream*, while near the wall of the vessel the flow is much slower, as indicated by the rate at which the pale blood-corpuscles are carried along in it. This is a purely physical phenomenon. If any liquid be forcibly driven through a fine tube which it wets, water for instance through a glass tube, the outermost layer of the liquid will remain motionless in contact with the tube; the next layer of molecules will move a little, the next faster still; and so on until a rapid current is found in the centre. If solid bodies, as powdered sealing-wax, be suspended in the water, these will all be carried on in the central faster current or *axial stream*, just as the red corpuscles are in the

artery. The white corpuscles, partly because of their less specific gravity, and partly because of their sometimes irregular form, due to amœboid movements, get frequently pushed out of the axial current, so that many of them are found in the inert layer.

Internal Friction. It follows from the above-stated facts that there is no noticeable friction between the blood and the lining of the vessel through which it flows: since the outermost blood-layer in contact with the wall of the vessel is changed only by diffusion. There is great friction between the different concentric layers of the liquid, since each of them is moving at a different rate from that in contact with it on each side. This form of friction is known in hydrodynamics as "internal friction," and it is of great importance in the circulation of the blood. Internal friction increases very fast as the calibre of the tube through which the liquid flows diminishes: so that with the same rate of flow it is disproportionately much greater in a small tube than in a larger one. Hence a given quantity of liquid forced in a minute through one large tube would experience much less resistance from internal friction than if sent in the same time through four or five smaller tubes, the united transverse sections of which were together equal to that of the single larger one. In the blood-vessels the increased total area, and consequently slower flow, in the smaller channels partly counteracts this increase of internal friction, but only to a comparatively slight extent; so that the internal friction, and consequently the resistance to the blood-flow, is far greater in the capillaries than in the small arteries, and in the small arteries than in the large ones. Practically we may regard the arteries as tubes ending in a sponge: the united areas of all the channels in the latter might be considerably larger than that of the supplying tubes, but the friction to be overcome in the flow through them would be much greater.

The Conversion of the Intermittent into a Continuous Flow. Since the heart sends blood into the aorta intermittently, we have still to inquire how it is that the flow in the capillaries is continuous. In the larger arteries it is not, since we can feel them dilating as the "*pulse*," on applying the finger over the radial artery at the wrist, or over the temporal artery on the side of the brow.

The first explanation which suggests itself is that since

the capacity of the blood-vessels increases from the heart to the capillaries, an acceleration of the flow during the ventricular contraction which might be very manifest in the vessels near the heart would become less and less obvious in the more distant vessels. But if this were so, then when the blood was collected again from the wide capillary sponge into the great veins near the heart, which together are but little bigger than the aorta, we ought to find a pulse, but we do not: the venous pulse which sometimes occurs having quite a different cause, being due to a back-flow from the auricles, or a checking of the on-flow into them, during the cardiac systole. The rhythm of the flow caused by the heart is therefore not merely cloaked in the small arteries and capillaries, but abolished in them.

We can, however, readily contrive conditions outside the Body under which an intermittent supply is transformed into a continuous flow. Suppose we have two vessels, *A* and *B* (Fig. 97). containing water and connected below in two ways: through the tube *a* on which there is a pump provided with valves so that it can only drive liquid from *A* to *B*; and through *b*, which may be left wide open or narrowed by the clamp *c*, at will. If the apparatus be left at rest the water will lie at the

Fig. 97.

same level, *d*, in each vessel. If now we work the pump, at each stroke a certain amount of water will be conveyed from *A* to *B*, and as a result of the lowering of the level of liquid in *A* and its rise in *B*, there will be immediately a return flow from *B* to *A* through the tube *b*. *A*, in these circumstances, would represent the venous system, from which the heart constantly takes blood to pump it into *B*, representing the arterial system; and *b* would represent the capillary vessels through which the return flow takes place; but, so far, we should have as intermittent a flow through the capillaries, *b*, as through the heart-pump, *a*. Now imagine *b* to be narrowed at one point so as to oppose resistance to the back-flow, while the pump goes on working steadily. The result will be an accumulation of water in *B*, and a fall of its level in *A*.
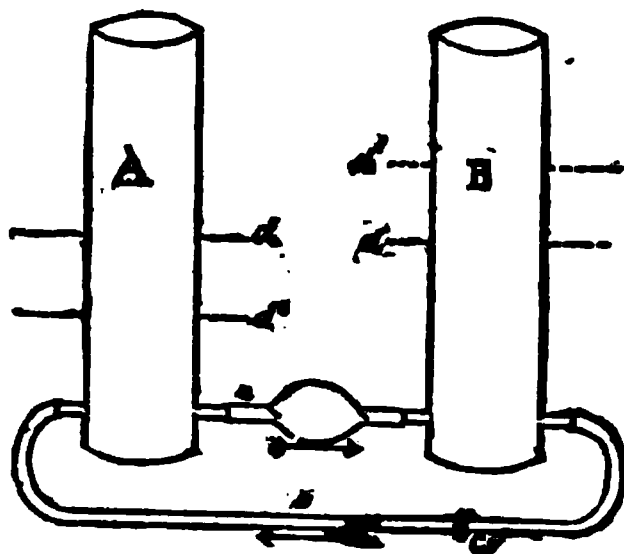
But the more the difference of level in the two vessels increases, the greater is the force tending to drive water back through *b* to *A*, and more will flow back, under the greater difference of pressure, in a given time, until at last, when the water in *B* has reached a certain level, *d'*, and that in *A* has correspondingly fallen to *d''*, the current through *b* will carry back in one minute just so much water as the pump sends the other way, and this back-flow will be nearly constant; it will not depend directly upon the strokes of the pump, but upon the head of water accumulated in *B*; which head of water will, it is true, be slightly increased at each stroke of the pump, but the increase will be very small compared with the whole driving force, and its influence will be inappreciable. We thus gain the idea that an incomplete impediment to the flow from the arteries to the veins (from *B* to *A* in the diagram), such as is afforded by internal friction in the capillaries, may bring about conditions which will lead to a steady flow along the latter vessels.

But in the arterial system there can be no accumulation of blood at a higher level than that in the veins, such as is supposed in the above apparatus; and we must next consider if the "head of water" can be replaced by some other form of driving force. It is in fact replaced by the elasticity of the large arteries. Suppose an elastic bag instead of the vessel *B* connected with the pump "*a*." If there be no resistance to the back-flow the current through *b* will be discontinuous. But if resistance be interposed, then the elastic bag will become distended, since the pump sends in a given time more liquid into it than it passes back through *b*. But the more it becomes distended the more will the bag squeeze the liquid inside and the faster will it send that back to *A*, until at last its squeeze is so powerful that each minute or two or five minutes it sends back into *A* as much as it receives. Thenceforth the back-flow through *b* will be practically constant, being immediately dependent upon the elastic reaction of the bag, and only indirectly upon the action of the pump which keeps it distended. Such a state of things represents very closely the phenomena occurring in the blood-vessels. The highly elastic large arteries are kept stretched with blood by the heart; and the reaction of their elastic walls, steadily squeezing on the blood in them, forces it continuously through the small arteries and capillaries. The steady flow in the latter depends

thus on two factors: first, the elasticity of the large arteries; and, secondly, the resistance to their emptying, dependent upon internal friction in the small arteries and the capillaries, which calls into play the elasticity of the large vessels. Were the capillary resistance or the arterial elasticity absent the blood-flow in the capillaries would be rhythmic.

CHAPTER XVI.

ARTERIAL PRESSURE. THE PULSE.

Weber's Schema. It is clear from the statements made in the last chapter that it is the pressure exerted by the elastic arteries upon the blood inside them which keeps up the flow through the capillaries, the heart serving to keep the big arteries tightly filled and so to call the elastic reaction of their walls into play. The whole circulation depends primarily, of course, upon the beat of the heart, but this only indirectly governs the capillary flow, and since the latter is the aim of the whole vascular apparatus, it is of great importance to know all about arterial pressure; not only how great it is on the average, but how it is altered in different vessels in various circumstances so as to make the flow through the capillaries of a given part greater or less according to circumstances; for, as blushing and pallor of the face (which frequently occur without any change in the skin elsewhere) prove, the quantity of blood flowing through a given part is not always the same, nor is it always increased or diminished in all parts of the Body at the same time. Most of what we know about arterial pressure has been ascertained by experiments made upon the lower animals, from which deductions are then made concerning what happens in man, since Anatomy shows that the circulatory organs are arranged upon the same plan in all the mammalia. A great deal can, however, be learnt by studying the flow of liquids through ordinary elastic tubes. Suppose we have a set of such (Fig. 98) supplied at one point with a pump, *c*, possessing valves of entry and exit which open only in the direction indicated by the arrows, and that the whole system is slightly overfilled with liquid so that its elastic walls are slightly stretched. These will in consequence press upon the liquid inside them and the amount of this pressure will be indicated by the gauges; so long as the pump is at rest it will be the same everywhere (and therefore equal in the gauges on *B* and *A*),

since liquid in a set of horizontal tubes communicating freely, as these do at *D*, always distributes itself so that the pressure upon it is everywhere the same. Let the pump *c* now contract once, and then dilate: during the contraction it will empty itself into *B* and during the dilatation fill itself from *A*. Consequently the pressure in *B*, indicated by the gauge *x*, will rise and that in *A* will fall. But very rapidly the liquid will redistribute itself from *B* to *A* through *D*, until it again exists everywhere under the same pressure. Every
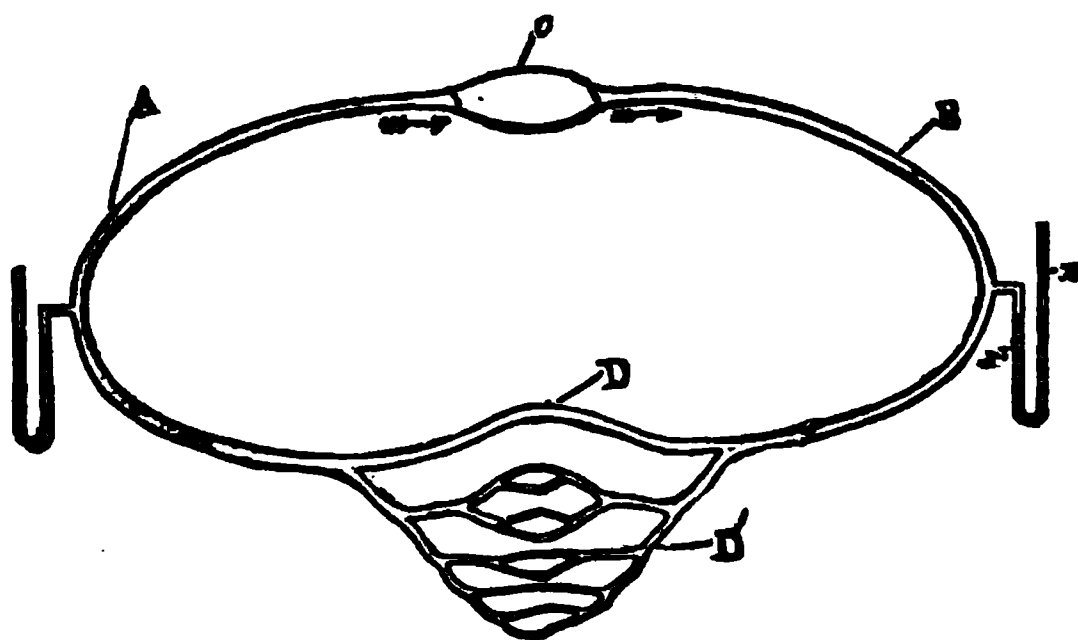
Fig. 96.—Diagram of Weber's Schema.

time the pump works there will occur a similar series of phenomena, and there will be a disturbance of equilibrium causing a wave to flow round the tubing; but there will be no steady maintenance of a pressure on the side *B* greater than that in *A*. Now let the upper tube *D* be closed so that the liquid to get from *B* to *A* must flow through the narrow lower tubes *D'*, which oppose considerable resistance to its passage on account of their frequent branchings and the great internal friction in them; then if the pump works frequently enough there will be produced and maintained in *B* a pressure considerably higher than that in *A*, which may even become negative. If, for example, the pump works 60 times a minute and at each stroke takes 180 cubic centimeters of liquid (6 ounces) from *A* and drives it into *B*, the quantity sent in at the first stroke will not (on account of the resistance to its flow offered by the small branched tubes), have all got back into *A* before the next stroke takes place, sending 180 more cubic centimeters (6 oz.) into *B*. Consequently at each stroke *B* will become more and more distended and *A* more and more emptied, and the gauge *x* will

indicate a much higher pressure than that on A. As B is more stretched, however, it squeezes harder upon its contents, until at last a time comes when this squeeze is powerful enough to force through the small tubes just 180 cubic centimeters (6 oz.) in a second. Then further accumulation in B ceases. The pump sends into it 10,800 cubic centimeters (360 ounces) in a minute at one end and it squeezes out exactly that amount in the same time from its other end; and so long as the pump works steadily the pressure in B will not rise, nor that in A fall, any more. But under such circumstances the flow through the small tubes will be nearly constant since it depends upon the difference in pressure prevailing between B and A, and only indirectly upon the pump which serves simply to keep the pressure high in B and low in A. At each stroke of the pump it is true there will be a slight increase of pressure in B due to the fresh 180 cub. cent. (6 oz.) forced into it, but this increase will be but a small fraction of the total pressure and so have but an insignificant influence upon the rate of flow through the small connecting tubes.

Arterial Pressure. The condition of things just described represents very closely the phenomena presented in the blood-vascular system, in which the ventricles of the heart, with their auriculo-ventricular and semilunar valves, represent the pump, the smallest arteries and the capillaries the resistance at D', the large arteries the elastic tube B, and the veins the tube A. The ventricles constantly receiving blood through the auricles from the veins, send it into the arteries, which find a difficulty in emptying themselves through the capillaries, and so blood accumulates in them until the elastic reaction of the stretched arteries is able to squeeze in a minute through the capillaries just so much blood as the left ventricle pumps into the aorta, and the right into the pulmonary artery, in the same time. Accordingly in a living animal a pressure-gauge connected with an artery shows a much higher pressure than one connected with a vein, and this persisting difference of pressure, only increased by a small fraction of the whole at each heart-beat, brings about a steady flow from the arteries to the veins. The heart keeps the arteries stretched and the stretched arteries maintain the flow through the capillaries, and the constancy of the current in them depends on two factors: (1) the resistance experi-

enced by the blood in its flow from the ventricles to the veins, and (2) the elasticity of the larger arteries which allows the blood to accumulate in them under a high pressure, in consequence of this resistance.

The Arterial Pressure. This cannot be directly measured with accuracy in man, but from measurements made on other animals it is calculated that in the human aorta its average is equal to that of a column of mercury 200 millimeters (8 inches) high. During the systole it rises about 5 millimeters ($\frac{1}{5}$ inch) above this and during the pause falls the same amount below it. The pressure in the venæ cavæ on the other hand is often negative, the blood being, to use ordinary language, often " sucked " out of them into the heart, and it rarely rises above 5 millimeters ($\frac{1}{5}$ inch) of mercury except under conditions (such as powerful muscular effort accompanied by holding the breath) which force blood on into the venæ cavæ and, by impeding the pulmonary circulation, interfere with the emptying of the right auricle. Hence to maintain the flow from the aorta to the vena cava we have an average difference of pressure equal to $200 - 5 = 195$ millimeters ($7\frac{1}{5}$ inches) of mercury, rising to $205 - 5 = 200$ mm. (8 inches) during the cardiac systole and falling to $195 - 5 = 190$ mm. ($7\frac{1}{5}$ inches) during the pause; but the slight alterations, only about $\frac{1}{20}$ of the whole difference of aortic and vena-cava pressures which maintain the blood-flow, are too small to cause appreciable changes in the rate of the current in the capillaries. The pressure on the blood in the pulmonary artery is about $\frac{1}{3}$ of that in the aorta.

Since the blood flows from the aorta to its branches and from these to the capillaries and thence to the veins, and liquids in a set of continuous tubes flow from points of greater to those of less pressure, it is clear that the blood-pressure must constantly diminish from the aorta to the right auricle; and similarly from the pulmonary artery to the left auricle. At any point, in fact, the pressure is proportionate to the resistance in front, and since the farther the blood has gone the less of this, due to impediments at branchings and to internal friction, it has to overcome in finishing its round, the pressure on the blood diminishes as we follow it from the aorta to the venæ cavæ. In the larger arteries the fall of pressure is gradual and small, since the amount of resistance met with in the flow through them is

but little. In the small arteries and capillaries the resistance overcome and left behind is (on account of the great internal friction due to their small calibre) very great, and consequently the fall of pressure between the medium-sized arteries and the veins is rapid and considerable.

Modifications of Arterial Pressure by Changes in the Rate of the Heart's Beat. A little consideration will make it clear that the pressure prevailing at any time in a given artery depends on two things—the rate at which the vessel is filled, i.e., upon the amount of work done by the heart; and the ease or difficulty with which it is emptied, that is, upon the resistance in front. A third factor has to be taken into account in some cases; namely, that when the muscular coats of the small arteries contract the local capacity of the vascular system is diminished, and has to be compensated for by greater distention elsewhere, and *vice versa.* This would of itself of course bring about changes in the pressure exerted on the contained liquid, but for the present it may be left out of consideration. Returning to the system of elastic tubes with a pump represented in Fig. 98, let us suppose the pump to be driving as before 10,800 cub. cent. (360 oz.) per minute into the tubes *B*, and that these latter are so distended that they drive out just that quantity in the same time. Under such conditions the pressure at any given point in *B* will remain constant, apart from the small variations dependent upon each stroke of the pump. Now, however, let the latter, while still sending in 180 cub. cent. (6 oz.) at each stroke, work 80 instead of 60 times a minute and so send in that time $180 \times 80 = 14,400$ cub. cent. (480 oz.) instead of the former quantity. This will lead to an accumulation in *B*, since its squeeze is only sufficient, against the resistance opposed to it, to send out 10,800 cub. cent. (360 oz.) in a minute. *B* consequently will become more stretched and the pressure in it will rise. As this takes place, however, it will press more powerfully on its contents until at last its distention is such that its elastic reaction is able to force out in a minute through the small tubes *D*, 14,400 cub. cent. (480 oz.) Thenceforth, so long as the pump beats with the same force and at the same rate and the peripheral resistance remains the same, the mean pressure in *B* will neither rise nor fall—*B* sending into *A* in a minute as much as *c* takes from it, and we would have a

steady condition of things with a higher mean pressure in *B* than before.

On the other hand, if the pump begins to work more slowly while the resistance remains the same, it is clear that the mean pressure in *B* must fall. If, for example, the pump works only forty times a minute and so sends in that time $180 \times 40 = 7200$ cub. cent. (240 oz.) into *B*, which is so stretched that it is squeezing out 10,800 cub. cent. (360 oz.), in that time, it is clear that *B* will gradually empty itself and its walls become less stretched and the pressure in it fall. As this takes place, however, it will force less liquid in a minute through the small tubes, until at last a pressure is reached at which the squeeze of *B* only sends out 7200 cub. cent. (340 oz.) in a minute; and then the fall of pressure will cease and a steady one will be maintained, but lower than before.

Applying the same reasoning to the vascular system, we see that (the peripheral resistance remaining unaltered), if the heart's force remains the same but its rate increases, arterial pressure will rise to a new level, while a slowing of the heart's beat will bring about a fall of pressure.

Modifications of Arterial Pressure Dependent on Changes in the Force of the Heart's Beat. Returning again to Fig. 98: suppose that, while the rate of the pump remains the same, its power alters so that each time it sends 200 cub. cent. (6.6 oz.) instead of 180 (6 oz.) and so in a minute 12,000 cub. cent (396 oz.) instead of 10,800 (360 oz.) —the quantity which *B* is stretched enough to squeeze out in that time. Water will in consequence accumulate in *B* until it becomes stretched enough to squeeze out 12,000 cub. cent. (396 oz.) in a minute, and then a steady pressure at a new and higher level will be maintained. On the other hand if the pump, still beating sixty times a minute, works more feebly so as to send out only 160 cub. cent. (5.6 oz.) at each stroke, then *B*, squeezing out at first more than it receives in a given time, will gradually empty itself until it only presses hard enough upon its contents to force $160 \times 60 = 9600$ cub. cent. (336 oz.) out in a minute.

Similarly, if while the resistance in the small arteries and capillaries remains the same and the heart's rate unchanged the stroke of the latter alters, so that at each beat it sends

more blood out than it did previously, then arterial pressure will rise; while if the heart beats more feebly it will fall.

Modifications of Arterial Pressure by Changes in the Peripheral Resistance. Let the pump c in Fig. 98 still work steadily sending 10,800 cub. cent. (360 oz.) per minute into B and the resistance increase, it is clear arterial pressure must rise. For B is only stretched enough to squeeze out in a minute the above quantity of liqnid against the original resistance, and cannot at first send out that quantity against the greater. Liquid will consequently accumulate in it until at last it becomes stretched enough to send out 10,800 cub. cent. (360 cubic oz.) in a minute through the small tubes, in spite of the greater resistance to be overcome. A new mean pressure at a higher level will then be established. If, on the contrary, the resistance diminishes while the pump's work remains the same, then B will at first squeeze out in a minute more than it receives, until finally its elastic pressure is reduced to the point at which its receipts and losses balance, and a new and lower mean pressure will be established in B.

Similarly in the vascular system, increase of the peripheral resistance by narrowing of the small arteries will increase arterial pressure in all parts nearer the heart, while dilatation of the small arteries will have the contrary effect.

Summary. We find then that arterial pressure at any moment is dependent upon—(1) the rate of the heart's beat; (2) the quantity of blood forced into the arteries at each beat; (3) the calibre of the smaller vessels. All of these, and consequently the capillary circulation which depends upon arterial pressure, are under the control of the nervous system (see Chap. XVII.).

The Pulse. When the left ventricle contracts it forces a certain amount of blood into the aorta, which is already distended and on account of the resistance in front cannot empty itself as fast as the contracting ventricle fills it. As a consequence its elastic walls yield still more—it enlarges both transversely and longitudinally and if exposed in a living animal can be seen and felt to pulsate, swelling out at each systole of the heart, and shrinking and getting rid of the excess during the pause. A similar phenomenon can be observed in all the other large arteries, for just as the contracting ventricle fills the aorta faster than the latter empties (the whole period of diastole and systole being required by

the aorta to pass on the blood sent in during systole), so the increased tension in the aorta immediately after the cardiac contraction drives on some of its contents into its branches, and fills these faster than they are emptying, and so causes a dilatation of them also, which only gradually disappears as the aortic tension falls before the next systole. Hence after each beat of the heart there is a sensible dilatation of all the larger arteries, known as the *pulse,* which becomes less and less marked at points on the smaller branches farther from the heart, but which in health can readily be recognized on any artery large enough to be felt by the finger through the skin, etc. The radial artery near the wrist, for example, will always be felt tense by the finger, since it is kept overfilled by the heart in the way already described. But after each heart-beat it becomes more rigid and dilates a little, the increased distension and rigidity gradually disappearing as the artery passes on the excess of blood before the next heart-beat. The pulse is then a wave of increased pressure started by the ventricular systole, radiating from the semilunar valves over the arterial system, and gradually disappearing in the smaller branches. In the aorta the pulse is most marked, for the resistance there to the transmission onwards of the blood sent in by the heart is greatest, and the elastic tube in which it consequently accumulates is shortest, and so the increase of pressure and the dilatation caused are considerable. The aorta, however, gradually squeezes out the excess blood into its branches, and so this becomes distributed over a wider area, and these branches having less resistance in front find less and less difficulty in passing it on; consequently the pulse-wave becomes less and less conspicuous and finally altogether disappears before the capillaries are reached, the excess of liquid in the whole arterial system after a ventricular systole being too small to sensibly raise the mean pressure once it has been widely distributed over the elastic vessels, which is the case by the time the wave has reached the small branches which supply the capillaries.

The pulse-wave travels over the arterial system at the rate of about 9 metres (29.5 feet) in a second, commencing at the wrist 0.159 second, and in the posterior tibial artery at the ankle 0.193 second, after the ventricular systole. The blood itself does not of course travel as fast as the pulse-wave, for

that quantity sent into the aorta at each heart-beat does not immediately rush on over the whole arterial system, but by raising the local pressure causes the vessel to squeeze out faster than before some of the blood it already contains, and this entering its branches raises the pressure in them and causes them to more quickly fill their branches and raise the pressure in them; the pulse-wave or wave of increased pressure is transmitted in this way much faster than any given portion of the blood. How the wave of increased pressure and the liquid travel at different rates may be made clearer perhaps by picturing what would happen if liquid were pumped into one end of an already full elastic tube, closed at the other end. At the closed end of the tube a dilatation and increased tension would be felt immediately after each stroke of the pump, although the liquid pumped in at the other end would have remained about its point of entry; it would cause the pulsation not by flowing along the tube itself, but by giving a push to the liquid already in it. If instead of absolutely closing the distal end of the tube one brought about a state of things more nearly resembling that found in the arteries by allowing it to empty itself against a resistance, say through a narrow opening, the phenomena observed would not be essentially altered; the increase of pressure would travel along the distended tube far faster than the liquid itself.

The pulse being dependent on the heart's systole, " feeling the pulse" of course primarily gives a convenient means of counting the rate of beat of that organ. To the skilled touch, however, it may tell a great deal more, as for example whether it is a readily compressible or "soft pulse" showing a low arterial pressure, or tense and rigid ("a hard pulse") indicative of high arterial pressure, and so on. In adults the normal pulse rate may vary from sixty-five to seventy-five, the most common number being seventy-two. In the same individual it is faster when standing than when sitting, and when sitting than when lying down. Any exercise increases its rate temporarily, and so does excitement; a sick person's pulse should not therefore be felt when he is nervous or excited (as the physician knows when he tries first to get his patient calm and confident), as it is then difficult to draw correct conclusions from it. In children the pulse is quicker than in adults, and in old age slower than in middle life.

The Rate of the Blood-Flow. As the vascular system

becoᵤes more capacious from the aorta to the capillaries the rate of flow in it becomes proportionately slower, and as the total area of the channels diminishes again from the capillaries to the venæ cavæ, so does the rate of flow quicken, just as a river current slackens when it spreads out, and flows faster where it is confined to a narrower channel; a fact taken advantage of in the construction of Eads' jetties at the mouth of the Mississippi, the object of which is to make the water flow in a narrower channel and so with a more rapid current in that part of the river. Actual measurements as to the rate of flow in the arteries cannot be made on man, but from experiments on lower animals it is calculated that in the human carotid the blood flows about 400 millimetres (16 inches) in a second. In the capillaries the current travels only from 0.5 to 0.75 mm. ($\frac{1}{50}$ to $\frac{1}{35}$ inch) in a second. The total time taken by a portion of blood in making a complete circulation has been measured by injecting some easily detected substance into an artery on one side of the body and noting the time which elapses before it can be found in a corresponding vein on the opposite side. In dogs this time is 15 seconds, and it is calculated for man at about 23 seconds. Of this total time about half a second is spent in the systemic and another half second in the pulmonary capillaries, as each portion of blood on its course from the last artery to the first vein passes through a length of capillary which on the average is 0.5 mm. ($\frac{1}{50}$ inch). The rate of flow in the great veins is about 100 mm. (4 inches) in a second, but is subject to considerable variations dependent on the respiratory and other movements of the Body; in the small veins it is much slower.

Secondary Causes of the Circulation. While the heart's beat is the great driving force of the circulation, certain other things help more or less—viz., gravity, compression of the veins, and aspiration of the thorax. All of them are, however, quite subsidiary; experiment on the dead Body shows that the injection of whipped blood into the aorta under a less force than that exerted by the left ventricle during life is more than sufficient to drive it round and back by the venæ cavæ. Not infrequently the statement is made in books that, probably, the systemic capillaries have an attractive force for arterial blood and the pulmonary capillaries for venous blood, but there is not the slightest evidence of the correctness of such a supposition, nor any necessity for making it.

The Influence of Gravity. Under ordinary circum-
stances this may be neglected, since in parts of the Body
below the level of the heart it will assist the flow in the ar-
teries and impede it equally in the veins, while the reverse
is the case in the upper parts of the Body. In certain cases,
however, it is well to bear these points in mind. A part
"congested" or gorged with blood should if possible be raised
so as to make the back-flow in its veins easier; and sometimes
when the heart is acting feebly it may be able to drive blood
along arteries in which gravity helps, but not otherwise. Ac-
cordingly in a tendency to fainting it is best to lie down. and
make it easier for the heart to send blood up to the brain,
bloodlessness of which is the cause of the loss of consciousness
in a fainting-fit. In fact, so long as the breathing continues,
the aspiration of the thorax will keep up the venous flow (see
below), while, in the circumstances supposed, a slight dimi-
nution in the resistance opposed to the arterial flow may be
of importance. The head of a person who has fainted should
accordingly never be raised until he has undoubtedly recov-
ered, a fact rarely borne in mind by spectators, who commonly
rush at once to lift any one whom they see fall in the street
or elsewhere.

The Influence of Transient Compression of the Veins.
The valves of the veins being so disposed as to permit only
a flow towards the heart, when external pressure empties a
vein it assists the circulation. Continuous pressure, as by
a tight garter, is of course bad, since it checks all subsequent
flow through the vessel; but intermittent pressure, such as is
exerted on many veins by muscles in the ordinary move-
ments of the Body, acts as a pump to force on the blood in
them.

The valves of the veins have another use in diminishing
the pressure on the lower part of those vessels in many
regions. If, for instance, there were no valves in the long
saphenous vein of the leg the considerable weight of the
column of blood in it, which in the erect position would be
about a metre (39 inches) high, would press on the lower part
of the vessel. But each set of valves in it carries the weight
of the column of blood between it and the next set of valves
above, and relieves parts below, and so the weight of the col-
umn of blood is distributed and does not all bear on any one
point.

Aspiration of the Thorax. Whenever a breath is drawn the pressure of the air on the vessels inside the chest is diminished, while that on the other vessels of the Body is unaffected. In consequence blood tends to flow into the chest. It cannot, however, flow back from the arteries on account of the semilunar valves of the aorta, but it can readily be pressed, or in common language "sucked," into the great veins close to the heart and into the right auricle of the latter. The details of this action must be omitted until the respiratory mechanism has been considered. All parts of the pulmonary circuit being within the thorax, the respiratory movements do not directly influence it, except in so far as the distention or collapse of the lungs alters the calibre of their vessels.

The considerable influence of the respiratory movements upon the venous circulation can be readily observed. In thin persons the jugular vein in the neck can often be seen to empty rapidly and collapse during inspiration, and fill up in a very noticeable way during expiration, exhibiting a sort of venous pulse. Every one, too, knows that by making a violent and prolonged expiration, as exhibited for example by a child with whooping-cough, the flow in all the veins of the head and neck may be checked, causing them to swell up and hinder the capillary circulation until the person becomes " black in the face," from the engorgement of the small vessels with dark-colored venous blood.

In diseases of the tricuspid valve another form of venous pulse is often seen in the superficial veins of the neck, since at each contraction of the right ventricle some blood is driven back through the right auricle into the veins.

Proofs of the Circulation of the Blood. The ancient physiologists believed that the movement of the blood was an ebb and flow, to and from each side of the heart, and out and in by both arteries and veins. They had no idea of a circulation, but thought pure blood was formed in the lungs and impure in the liver, and that these partially mixed in the heart through minute pores supposed to exist in the septum. Servetus, who was burnt alive by Calvin in 1553, first stated that there was a continuous passage through the lungs from the pulmonary artery to the pulmonary veins, but the great Englishman Harvey first, in lectures delivered in the College of Physicians of London about 1616, demonstrated that the movement of the blood was a continuous circulation as we

now know it, and so laid the foundation of modern Physi-ology. In his time, however, the capillary vessels had not been discovered, so that although he was quite certain that the blood got *somehow* from the final branches of the aorta to the radicles of the venous system, he did not exactly know *how*.

The proofs of the course of the circulation are at present quite conclusive, and may be summed up as follows: (1) Blood injected into an artery in the dead Body will return by a vein; but injected into a vein will not pass back by an artery. (2) The anatomical arrangement of the valves of the heart and of the veins shows that the blood can only flow *from* the heart, through the arteries and back *to* the heart by the veins. (3) A cut artery spurts from the end next the heart, a cut vein bleeds most from the end farthest from the heart. (4) A portion of a vein when emptied fills only from the end farthest from the heart. This observation can be made on the veins on the back of the hand of any thin per-son, especially if the vessels be first gorged by holding the hand in a dependent position for a few seconds. Select then a vein which runs for an inch or so without branching, place a finger on its distal end, and then empty it up to its next branch (where valves usually exist) by compressing it from below up. The vessel will then be found to remain empty as long as the finger is kept on its lower end, but to fill im-mediately when it is removed; which proves that the valves prevent any filling of the vein from its heart-end backwards. (5) If a bandage be placed around the arm, so as to close the superficial veins, but not tight enough to occlude the deeper-seated arteries, the veins on the distal side of the bandage will become gorged and those on its proximal side empty, showing again that the veins only receive blood from their ends turned towards the capillaries. (6) In the lower animals direct observation with the microscope shows the steady flow of blood from the arteries through the capillaries to the veins, but never in the opposite direction.

CHAPTER XVII.

THE NERVES OF THE HEART, AND SOME PHYSIOLOGICAL PECULIARITIES OF CARDIAC MUSCLE.

The Co-ordination of Heart and Arteries. We have hitherto considered the working of the vascular system as if it were a mere mechanical hydraulic apparatus; and such in a certain sense it is, and by so regarding it many of the phenomena of the blood-flow can be explained. But life is a constant adjustment to constantly varying conditions, and the higher the organism the more numerous the conditions which influence it and the greater its power of adapting itself to them; and this adaptability, this continuous self-adjustment, is nowhere better exhibited than in the heart and blood-vessels.

The object to be attained is the maintenance of an orderly current in the capillaries in accordance with the needs of the whole Body and of each of its organs at the time. This clearly calls for some means of interaction between heart and blood-vessels: should the heart beat and the arteries relax or contract, each without reference to the other, no steady capillary flow could result. To secure such a flow the work done by the heart and the resistance offered in the vessels must at all times be correlated; so that the heart shall not by too powerful action over-distend or perhaps burst the small arteries, nor the latter contract too much and so, by increasing the peripheral resistance, raise aortic pressure to a great height and increase unduly the work to be done by the left ventricle in forcing open the semilunar valves.

Further, the total amount of blood in the Body is not sufficient to keep all its organs simultaneously supplied with the amount needful for the full exercise of their activity; in fact the blood-vessels of the spleen, liver, and alimentary canal, if all fully distended, can themselves contain almost the whole blood of the Body, so that by paralyzing their coats in an animal it can be caused to faint, or even be killed, by what has been

called an "internal bleeding," due to the accumulation of so much blood in the vessels of the abdomen that not enough is left over for the supply of the brain and other parts. In the Body, accordingly, we never find all its parts hard at work at the same moment. If when one group of muscles was set at work and needed an extra blood-supply, this should be provided merely by increasing the heart's activity and keeping up a faster blood-flow everywhere throughout the Body, there would be a clear waste—much as if the chandeliers in a house were so arranged that when a larger flame was wanted at one burner it could only be obtained by turning more gas on at all the rest at the same time; besides the big tap at the gas-meter regulating the general supply of the house, local taps at each burner are required which regulate the gas-supply to each flame independently of the others. A corresponding arrangement is found in the Body. Certain nerves control the calibre of the arteries supplying different organs and, when the latter are set at work, cause their arteries to dilate and so increase the amount of blood flowing through them, while the general circulation elsewhere remains practically unaffected. The resting parts at any moment thus get enough blood to maintain their healthy nutrition and the working parts get the larger quantity required to make good used-up material and to wash out wastes: as certain organs come to rest and others are set in activity, the arteries of the former narrow and of the latter dilate; in this way the distribution of the blood in the Body is undergoing constant changes, parts which at one time contain much blood at another having but little. In addition, then, to nervous organs regulating the work of the heart and the arteries with reference to one another, we have to consider another set of vascular nerves which govern the local blood-supply of different regions of the Body. How important this is may be illustrated by considering what happens when the surface of the Body is exposed for some time to cold. The skin normally contains much blood, brought to it in part to be cooled; but under the supposed conditions the loss of heat would soon be so great as to be harmful did not small arteries of the skin contract, as is indicated by its pallor, and thus lessen the blood-flow through it. This contraction is not chiefly, if at all, due to direct action of the cold on the vessels, but to the stimulation of cutaneous afferent nerves which excite a nerve-

centre from which efferent impulses are in turn sent to the muscular coat of the cutaneous arteries. The blood driven from the skin must find a place elsewhere in the circulatory system, and so internal organs tend to become over-full and at the same time general arterial pressure is raised. This, again through nerves, acts upon the heart, and alters its rate of beat for a time. But in health some internal arteries soon dilate sufficiently to compensate for the constriction of the surface vessels, and arterial pressure and the pulse again become normal, though with a less proportion of the total blood flowing through the skin than before: this readjustment is brought about entirely through nerves and nerve-centres placing all the arteries in connection with one another and with the heart, so that they exert a mutual control. If the cold be not too prolonged its cessation is followed by a return of the blood-flow to its original condition, this action being brought about by cardiac and vascular nerve apparatuses. We have to mainly consider in this and the succeeding chapter the nerves which regulate the heart-beat and those which influence the calibre of arteries; but it is necessary first to study the muscular tissue of the heart more thoroughly than we have hitherto done.

Some Physiological Peculiarities of Cardiac Muscle. We have already seen that the muscular tissue of the heart, though striped, differs considerably in structure from the tissue of the skeletal muscles: it differs also somewhat in properties, and as the latter differences can be most readily studied on the heart of the frog, which will beat for a long time after excision, it will be best to commence with that. The frog's heart consists of four contractile chambers through which the blood flows successively, as is indicated in the diagram, Fig. 99, in which no attempt has been made to indicate the actual appearance of the organ, which is in fact curved on itself somewhat in the form of a capital ⋉ (see *Z*, Fig. 99), and this is also the shape of the mammalian heart in an early stage of embryonic development. The main chambers are incompletely separated by constrictions, at some of which valves are placed, and are in order—the *venous sinus*, *A*, receiving blood from the systemic veins; the *atrium*, consisting of two auricles, *B, C*, of which the right is much the larger and is supplied from the sinus, while the left gets blood from the small pulmonary veins, *pv*; the *ventricle, D,* sup-

plied from both auricles and having projecting into it the two flaps of the auriculo-ventricular valve, which are continued from the end of the *septum* or partition lying between the auricles; the *bulbus arteriosus*, *E*, from which the systemic and pulmonary arteries are supplied. To describe the very interesting mechanism by which the arterial and venous blood supplied to the single ventricle are kept separate and sent from the arterial bulb through different channels would take us beyond the limits of this book, but it is well worth study in some treatise on comparative physiology.

The muscular tissue of the frog's heart consists of cells which are in form somewhat like those of involuntary muscle, but they are frequently forked at their ends, and they are obscurely cross - striped like human cardiac muscle (Fig. 123). The main thickness of the walls of all the chambers of the heart consists of this muscle, and is known as the *myocardium*. It commences on the ends of the great veins near where they join the heart, and is thence continued to the roots of the great arteries arising from the bulb; but it is thinner at the constrictions which lie between the main cavities than elsewhere, and there is ar-
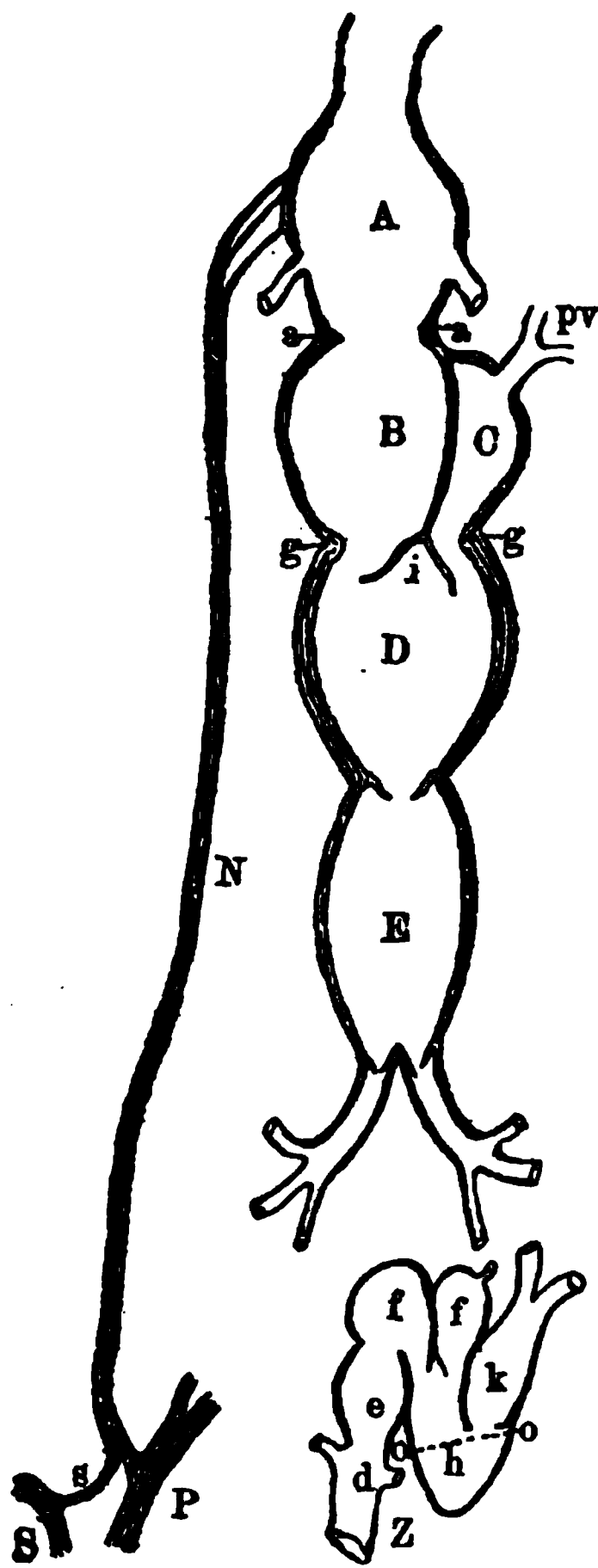
Fig. 99.—Diagram of the frog's heart. *A*, venous sinus; *B, C*, right and left auricles, together forming the atrium; *p.v.*, pulmonary veins; *a, a*, constriction between sinus and atrium; *D*, ventricle; *g. g*, constriction between auricles and ventricles; *i*, auriculo-ventricular valve; *E*, arterial bulb; *P*, pneumogastric or vagus nerve; *S*, sympathetic nerve; *N*, cardiac nerve containing fibres from both vagus and sympathetic. *Z* shows the natural relative positions of the chief chambers of the heart: *d*, vena cava; *e*, venous sinus; *f, f*, auricles; *h*, ventricle; *k*, arterial bulb.

ranged in rings around the openings.

A single nerve, *N*, goes to the heart from each side (only that of the right side is represented in the diagram). This nerve is usually spoken of as the *cardiac branch* of the vagus or pneumogastric, *P*, but it is partly made up of fibres from the sympathetic nerve, *S*, which join the pneumogastric close to the skull and run on with its cardiac branch, the two forming the apparently single nerve-trunk, *N*, which runs to the venous sinus, breaking up near it into several twigs. On these twigs and in the plexus which they form in the wall of the sinus are numerous nerve-cells, forming the *sinus ganglion* or *ganglion of Remak*. From the sinus nerves run down the walls of the auricles to the auriculo-ventricular groove, *g*, and two comparatively large twigs pass down the auricular septum to the region of the valve, *i*, and there enter a collection of nerve cells which, with other cells lying in the groove, constitute the *auriculo-ventricular* or *Bidder's ganglion*. From that ganglion nerves are continued to the wall of the ventricle, and near its base have nerve-cells mixed with them. A few nerve-cells are also found among the fibres running down the auricular septum: in the apex of the ventricle, however, and in the bulb there are no ganglion-cells, though nerve-fibres are present. We find then a considerable collection of nerve-cells in the walls of the venous sinus, a few cells in the auricular septum, a considerable collection at the junction of atrium with ventricle, and a few scattered cells in the neighboring portions of the ventricle. The cells of the ganglion of Remak and some of those in the septum belong to a type differing somewhat from those hitherto described. Each is pear-shaped, and has a conspicuous nucleus with a nucleolus; from the narrow end of the cell proceeds a branch which ultimately becomes the axis cylinder of a medullated nerve-fibre. Another branch arises by two or more roots which coil spirally around the straight branch, and finally unite and proceed as a non-medullated fibre. Most of the remaining nerve-cells of the frog's heart are spindle-shaped, and receive a nerve-fibre at one end and give one off at the other. They are known as *bipolar* cells. The cardiac nerve, *N*, Fig. 99, contains both gray and medullated fibres, the latter coming entirely or almost entirely from its vagus root; as the fibres passing on from the sinus ganglion to the ganglion of Bidder contain very few medullated fibres, it is probable that many of the vagus fibres end in the pear-shaped

cells from which gray fibres are given off to the rest of the heart, mingled with the original gray fibres derived from the sympathetic: in the ventricle and bulb only non-medullated fibres are found.

The Beat of the Frog's Heart. When both cardiac nerves are cut in a frog the heart continues its regular rhythmic beat, as it does also when carefully removed from the body of the animal: this makes it clear that whatever initiates the beat lies in the heart itself, which must therefore be regarded as an automatic organ; but leaves it still uncertain whether the exciting cause of each beat is to be sought in the nervous elements of the heart or in the cardiac muscle itself. Arguing from the analogy of ordinary striped muscle, which is not automatic, one would be inclined to ascribe to the nerve-cells of the isolated heart the origination of nervous impulses for the myocardium, and certain experiments tend to support this view; but cardiac muscle differs considerably from the skeletal muscles in its histology, so it is unsafe to argue from one to the other, and some experiments show that we must ascribe to it, in addition to contractility, a certain amount of automaticity and of conductivity and co-ordinating power. In physiological properties it combines the characteristic properties of fully differentiated nerve-cell and nerve-fibre with those of muscle-fibre.

Each beat of the heart of the frog can be seen to commence where the great veins enter the venous sinus, and from there to spread rapidly over the whole sinus; then there is a brief check, and the atrium beats; then another check, followed by the beat of the ventricle; finally, again after a very short pause, comes the contraction of the arterial bulb: then the series of phenomena is repeated in the same unvarying order as long as the heart is in good condition and is left to itself. The fact that each cycle of contractions begins at the mouths of the *venæ cavæ* and the sinus, where nerve-cells are very numerous, and passes on to the ventricle, where they are few, and to the bulb, where there are none, has been taken as an evidence of the origination of each beat through stimuli developed in cardiac nerve-cells; and this opinion gains support from what is usually seen on an excised heart when it is gradually dying. The bulb and ventricle cease to beat first, then the auricles, last the sinus, and this although the ventricle may still be contractile and able to give a good beat or

a set of several beats when directly stimulated, as by pricking or by induction shocks. The loss of irritability as the heart dies also usually appears in the same order: when the ventricle and auricle have both ceased to beat, it is frequently possible to excite the auricle by a direct stimulation which is powerless when applied to the ventricle; and when the whole heart has ceased to pulsate the venous sinus will sometimes respond to direct stimulation when auricle and ventricle will not. Still further, if the heart be carefully divided at the level *aa*, Fig. 99, so as to separate the sinus from the rest, the usual result is that the sinus goes on beating, but the rest of the heart lies for a time at rest: soon it begins to beat quite rhythmically, but at a slower rate than the separated sinus. If the cross-section be made at the level *gg* so as to separate the sinus and auricle from the rest, they go on beating, but the ventricle and bulb usually lie quiescent for a considerable time, and then commence. On account of the anatomical relations of the parts (*Z*, Fig. 99) it is not possible to completely separate the ventricle from the sinus without doing injury to the former; but if the lower third of the ventricle (which contains no nerve-cells) be cut off from the rest of the heart along the line *oo*, this separated portion never begins to beat spontaneously,

Fig. 100.—Diagram of a perfusion cannula tied into the separated apex of the ventricle of a frog's heart for the purpose of circulating liquids through it: *a*, inflow; *b*, outflow, division of cannula.

though the remainder of the heart continues its pulsations. So far the case for the view that the nerve-cells take the initiative in the changes which result in a normal beat, and that cardiac muscle is not automatic, is a strong one; but other facts show that it cannot be accepted without modification.

Although the separated apex of the ventricle of the frog, left to itself, does not beat, yet it can be made to beat without the application to it of anything that we are justified in calling a stimulus: it does under certain conditions exhibit automaticity. If it be tied on the end of a tube divided by a partition (Fig. 100), and some blood or blood-serum be circulated through it, in from *a* and out by *b*, under a slight pressure, this bit of ventricle, devoid of nerve-cells, after a time begins to beat rhythmically. It has been suggested that in
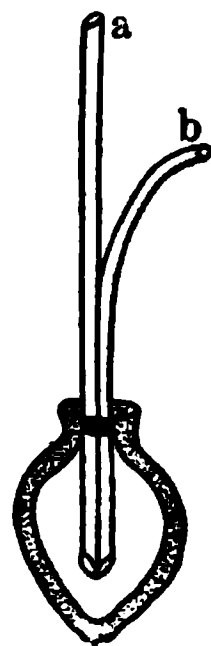
this case the distension of the muscle or some chemical constituent of the liquid acts as a stimulus; but in no other muscle do we find blood-supply or mere stretching act as a stimulus, and if they are to be assumed as so acting in this case their action is uniform, while the resulting contractions are interrupted and rhythmic: moreover, they are co-ordinated; they are not irregular twitches first of one bundle of the myocardiac fibres and then of another, but duly combined, so as by their mutual action to empty the cavity they surround. The evidence thus obtained as to the possession of some automatic and some co-ordinative properties by the frog's cardiac muscle is strengthened by experiments on the hearts of tortoises and terrapins. In those animals the apical portions of the ventricle are devoid of nerve-cells, yet narrow strips of them hung up and slightly loaded will usually begin to beat after a time. If they do not, all that is necessary is to stimulate them rhythmically for a short time; then on ceasing the stimulation the rhythmic contractions continue. Here, no doubt, the loading is a favoring condition, but so it is for the activity of ordinary muscles, on which, nevertheless, it does not act as a stimulus.

The conclusion to which we are led is that the muscle-cells of the frog's heart have retained to some extent those automatic and co-ordinating faculties of undifferentiated protoplasm which the more highly evolved fibre of skeletal muscle has lost. We find in the presence of certain of the nerve-cells of the heart a highly favorable condition for the exhibition of those powers: the nerve-elements perhaps influence the nutrition, perhaps in some other mode affect the molecular structure of the muscle-cells connected with them so as to favor spontaneous contraction, but, like stretching the isolated strip of ventricle, they merely bring about a state of things promoting the exercise of powers inherent in the cardiac muscle tissue itself.

The evidence as to the automaticity of the muscle of the mammalian heart is not quite as full as in the case of the frog. In it also there are collections of ganglion-cells where the great veins join the auricles and near the base of the ventricles; but there are others in the apical region of the ventricles, so it is not possible to examine an isolated apex free from ganglion-cells as it is in the frog. The musculature of the auricles is prolonged for some little way on the ends of the

venæ cavæ and the pulmonary veins, and there each normal beat commences, the contraction spreading rapidly over the whole auricle and thence to the ventricle without the brief intermediate pause observable in the frog. In the mammal, also, the ventricles if supplied with blood from the auricles go on beating although all nerve and muscular continuity between auricle and ventricle has been destroyed, by passing rigid tubes through the auriculo-ventricular openings and then tying a ligature tight on the outside of the heart along the auriculoventricular groove, so as to crush the tissues between the string and the tubes. If the ligatures be so placed as not to impede the flow in the coronary vessels the ventricles beat long and powerfully, but with a rhythm independent of that of the auricles and usually slower. Also when the mammalian heart is dying slowly, as in a suffocated animal, the auricles usually continue to beat after the ventricle has ceased, the small dog's-ear-shaped projection of the auricles (which it may be noted has given its name to the whole *auricle*) usually being the last portion to come to rest, especially that on the right side, which was accordingly named *ultima moriens* by the old physiologists. On the whole we are perhaps justified in assuming that the myocardium of the mammal is automatic, like that of the frog, and that in it also the presence and influence of ganglion-cells favor the production of a beat, but do not initiate it.

The muscle of the frog's heart is, we have seen, co-ordinative: the isolated ventricular apex can perform a regular beat. It is probable that this is not the case in the mammal. When a dog's heart is injured the ventricles sometimes cease to give true beats though the muscle bundles constituting them go on contracting, but it is with no combined action such as would empty the ventricle. Irregular and useless contractions travel simultaneously over the myocardium in various directions, so that the whole mass seems trembling. Such a state (known as "fibrillar contraction") is especially apt to follow wounds in the region of the main nerve-trunks running down the ventricles alongside the larger branches of the coronary arteries, and is probably due to the injury of some nervous apparatus concerned in securing the proper co-ordinated contractions of the normal beat. In many other regions wounds may be inflicted on the ventricle with considerable impunity.

The Heart-beat is not a Tetanic Contraction. We have seen that it is possible by rapidly succeeding stimuli to throw the skeletal muscles into a prolonged and apparently continuous contraction, and that there is good reason, afforded by the phenomena of "secondary tetanus," for the belief that all normal contractions of the voluntary muscles are compound or tetanic contractions. This is not the case with the heart. It is possible by repeated stimuli to hurry the beat of a frog's heart, but not to fuse two or more beats into a single longer uninterrupted contraction. And as regards the normal beat of the heart, experiments as to secondary tetanus prove the same thing. If the heart of an anæsthetized dog or other mammal be carefully laid bare and the nerve of a nerve-muscle preparation be laid on it, we get for each beat a single twitch of the signal muscle, and not a short tetanus lasting as long as the ventricular contraction, such as must arise were this contraction tetanic.

The Ventricular Contraction is always Maximal. It has been pointed out with reference to the skeletal muscles that within limits the extent of a contraction varies with the stimulus used: a feeble stimulus giving a small contraction, a stronger a greater. This is not the case with cardiac muscle. A quiescent ventricle or strip of ventricle taken from the heart of a frog or turtle can often be made to contract by stimulation; but provided the stimulus is powerful enough to cause a beat at all, it always causes the fullest contraction the piece of heart is capable of at the time. Increase of stimulus causes no increase of contraction. There is good reason to believe that in the physiological working of the ventricles of the mammalian heart each completely expels during its contraction all the blood contained in it: the papillary muscles pulling down the flaps of the auriculo-ventricular valves so that they finally form a cone on which the rest of the ventricular boundaries can fit closely so as to obliterate the cavity they enclose. This being so, the quantity of blood driven into the arteries by each contraction of the ventricles depends on the amount in the latter when their beat commences. This amount depends partly upon the quantity of blood returned from the great veins during the preceding diastole and partly upon the force with which the auricles contract, for they, although each contraction is probably maximal for their condition at the time being, do

not completely empty themselves at each stroke; they sometimes do so more completely and sometimes less. In this manner the auricles can to a great extent control the work done by the ventricles, through influencing the amount of blood in the latter at the commencement of the ventricular systole: more complete relaxation of the auricles during diastole promotes inflow from the great veins, more extensive contraction during auricular systole more completely fills the ventricles. As we shall see, the force and rate of the auricular beat is much more under the control of nerves reaching the heart from other parts than is that of the ventricles. The auricles are a feed-pump adjusting their work, and through it the work of the whole heart, to the general condition of the Body; the ventricles are a grosser force-pump driving on whatever blood is supplied to them, be it much or be it little.

The Extrinsic Nerves of the Mammalian Heart. As in the frog, these come from two sources, at least so far as indicated by gross anatomy. Their exact anatomical arrangement differs in various mammals, as the rabbit, dog, and man, and even somewhat in different individuals of these species, but in the main is the same. The pneumogastric gives off from its main stem in the neck several cardiac branches; so do the lower cervical and the upper thoracic ganglia of the sympathetic chain. Both sets intermingle, and near the heart end in plexuses containing nerve-cells; from these plexuses nerves are distributed to that organ. In the heart itself, as already stated, are collections of ganglion-cells in the auricles near the ends of the great veins, near the base of the ventricles, and a few cells scattered over the ventricles even in their apical regions. The nerve-fibres coming through the pneumogastrics are medullated and consist of a set of small fibres and a group of large: the smaller lose their medulla in ganglion-cells in or near the heart; the larger retain the medullary sheath, and may be traced even over the ventricles, which in this respect differ from that of the frog; the fibres supplied from the sympathetic are non-medullated. Broadly speaking, the nerve-fibres fall into three physiological sets corresponding to the three anatomical varieties: the small medullated fibres are efferent and inhibitory—when excited they slow the heart-beat; the large medullated are in part at least afferent, conveying to the central nervous system impulses which originate in the heart; the sympathetic fibres are efferent and excitor, and

when stimulated quicken or strengthen the heart beat. The afferent fibres will be more conveniently studied in connection with nerves of the blood-vessels (Chap. XVIII).

The Cardio-inhibitory Fibres. These, though running in the neck in what seems to be the main pneumogastric trunk, do not leave the skull in that nerve, but in the spinal accessory (XI cranial nerve), which, it will be remembered, arises in part from the brain and in part from the upper portion of the spinal cord. That nerve gives off near the brain a small branch which joins the pneumogastric and runs on in it to near the heart. The fibres may be tracked in the pneumogastric by their small size, but more satisfactorily by the Wallerian method. It is then found—1, when the main pneumogastric trunk is divided in the neck all the medullated fibres in it distal to the place of section degenerate; 2, if only the branch joining the spinal accessory to the pneumogastric be cut, then only some fibres in the pneumogastric stem degenerate, and these fibres are the small medullated set; 3, if the pneumogastric alone be divided above the point where the branch from the spinal accessory joins it, then the large medullated fibres of the cardiac branches of the vagus degenerate, but the small do not. Hence we conclude that the small fibres come through the accessory. Physiological experiment confirms this. Immediately after cutting the main pneumogastric trunk stimulation of its peripheral end checks the beat of the heart; but if the stimulation be applied after several days, it has no effect on the heart. If instead of cutting the whole pneumogastric stem we divide only the branch going to it from the accessory, we find similar results: after two or three days (i.e., when the microscope reveals degeneration of the small medullated fibres in the main stem, all the rest being in their normal condition) stimulation of it is as absolutely without direct effect on the heart as after complete degeneration of the whole nerve-trunk. In the frog there is no separate spinal accessory nerve; the cardio-inhibitory fibres pass from the brain directly into the pneumogastric; but in both frog and mammal their centre lies in a group of nerve-cells of the medulla oblongata known as the *cardio-inhibitory centre.*

The cardiac nerve of the frog consists (Fig. 99) of a pneumogastric and a sympathetic portion: if it be stimulated the usual result is that the heart is slowed when the stimulus is

feeble, and is stopped when the stimulus is more powerful; and in this animal it is possible by carefully applied stimulation to keep the heart at rest for a considerable time, during which it lies distended and flabby; but nearly always it ultimately recommences its beat even though the stimulation of the nerve be continued. During its *inhibition* the heart is irritable and contractile, for it beats if a direct stimulus be applied to it: the myocardium is therefore not incapable of action; but either some influence normally proceeding from its nerve-cells and promoting its automatic contraction is prevented, or the stimulation directly acts on the cardiac muscle and for the time lowers or removes its spontaneity. If the stimulus applied to the cardiac nerve be not strong enough to completely inhibit the heart, it is usually seen that the pulsations are not only fewer, but more feeble; but this is not always the case : the beats may be slower and not less powerful than before, or they may continue with the same rhythm, but be less powerful; in any case the result is to diminish for the time the work done by the heart.

In mammalia the phenomena are essentially the same. If artificial respiration be maintained in an anæsthetized rabbit and its heart laid bare, and then the pneumogastric trunk be divided on one side of the neck and its cardiac end stimulated, the heart comes to rest, distended and soft to the touch; or, with more feeble stimulation, the pulsations are slowed; or they may be both slower and feebler, or feebler and not slower; but the amount of blood driven out by the ventricles in a given time is usually much less. When the beat is only weakened it often happens that the effect shows itself much more markedly on the auricles than on the ventricles, though this of course diminishes the work done by the ventricles, as they are then supplied with less blood to pump on; and occasionally it may be seen that the auricles miss a beat, giving only one for each two of the ventricles, quite contrary to the case of a dying heart, in which, as we have seen, the auricular beat is more prominent. This illustrates the fact that the auricles are more sensitive to external nervous control than the ventricles, and provide, so to speak, the " fine adjustment" of the cardiac apparatus.

Whether the heart is stopped or slowed or its beats weakened, the result must be a fall in arterial pressure, for the stretched arteries go on driving blood through the capillaries

to the veins, while their supply from the heart is cut off or lessened. Hence a pressure-gauge attached to an artery shows readily the influence of stimulation of the cardio-inhibitory fibres; and in order to avoid the serious operation of opening the thorax to observe the heart directly, it is usual to study indirectly the cardiac effect of stimulation of the pnemogastric by observing its influence on arterial pressure.
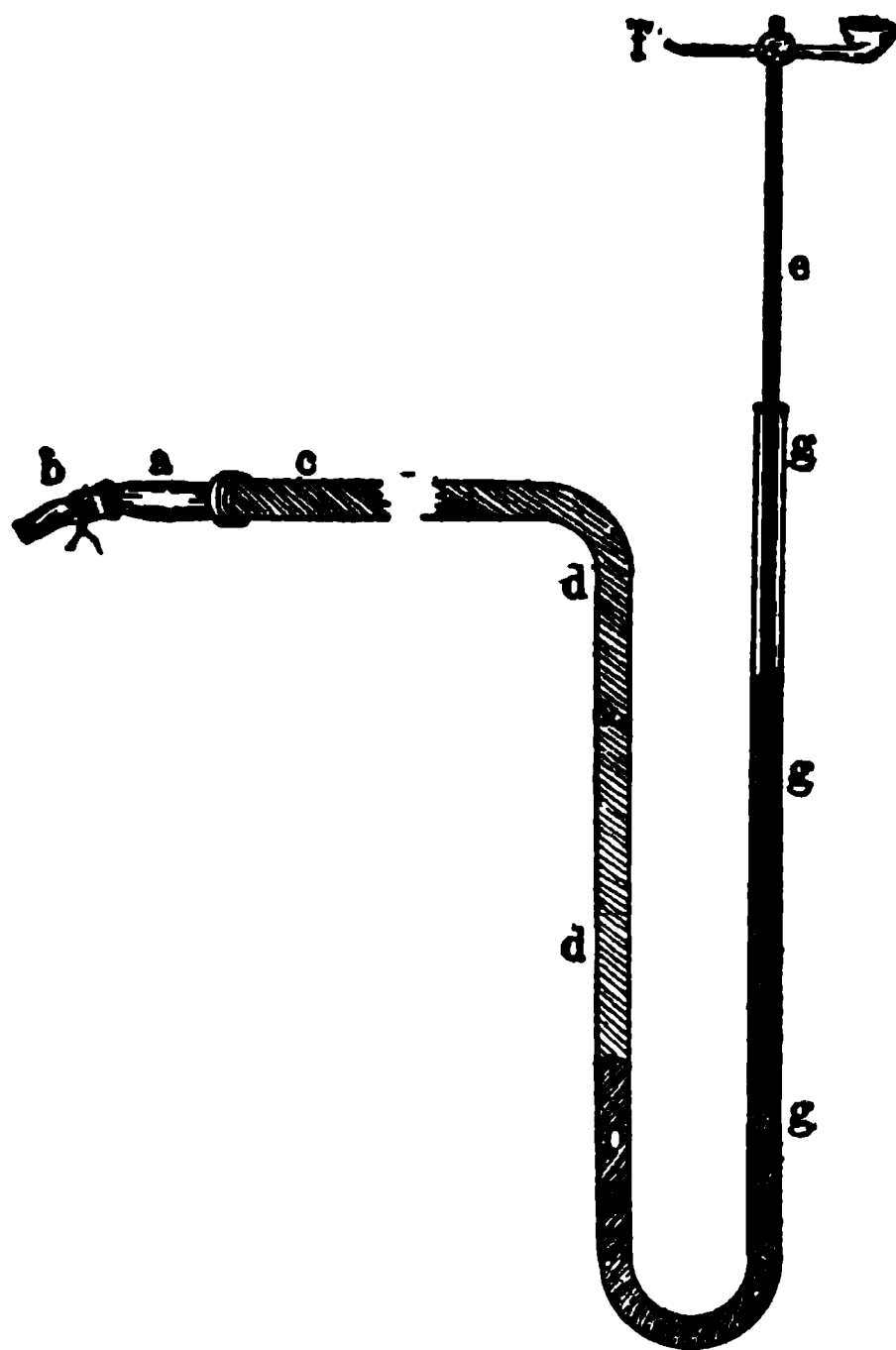

FIG. 101.—Manometer for recording variations in arterial pressure. *ddgcg.* glass U-tube partly filled with mercury. *o;* its limb. *gg,* is open to the air, and a float bearing the light stem *e* on which is the pen *f* rests on the mercury. the limb *dd* is filled above the mercury with magnesium sulphate solution and connected water-tight by tubes and the cannula *a* with the heart end of a divided artery. The pen writes on a horizontally travelling surface and rises and falls with the mercury on the side *gg.* a rise indicating increase of arterial pressur, a fall the reverse: the pressure in the artery at any moment is indicated by the vertical distance between the top of the mercury in *dd* and that in *gg.* due allowance being made for the weight of the magnesium sulphate and some other possible sources of error.

For this purpose a small glass tube or *cannula*, *a*, filled with solution of magnesium sulphate (to check blood-clotting) is introduced into the cardiac end of a divided artery, say the femoral, of a living animal, the artery being clamped at a place nearer the heart than the point where the cannula is tied on.

The cannula is (Fig. 101) connected by an inelastic tube, *c*, of convenient length, also filled with magnesium sulphate, to one end of a U-shaped glass pressure-gauge or *manometer*, *ddgg*, containing mercury. On the top of the mercury in the limb *gg* of the manometer floats a light stem *e* carrying a pen which writes on a travelling surface. Above the mercury, *o*, on the side *dd*, the tube is filled with magnesium sulphate solution. When the pressure on each side of the manometer is alike the mercury stands at the same level in both limbs, but when it is increased on the side *dd* by taking the clamp off the artery and throwing in the pressure of the blood the mercury in *gg* rises, carrying the float and pen with it and draws a line such as that at *yz*, Fig. 102, on the travelling
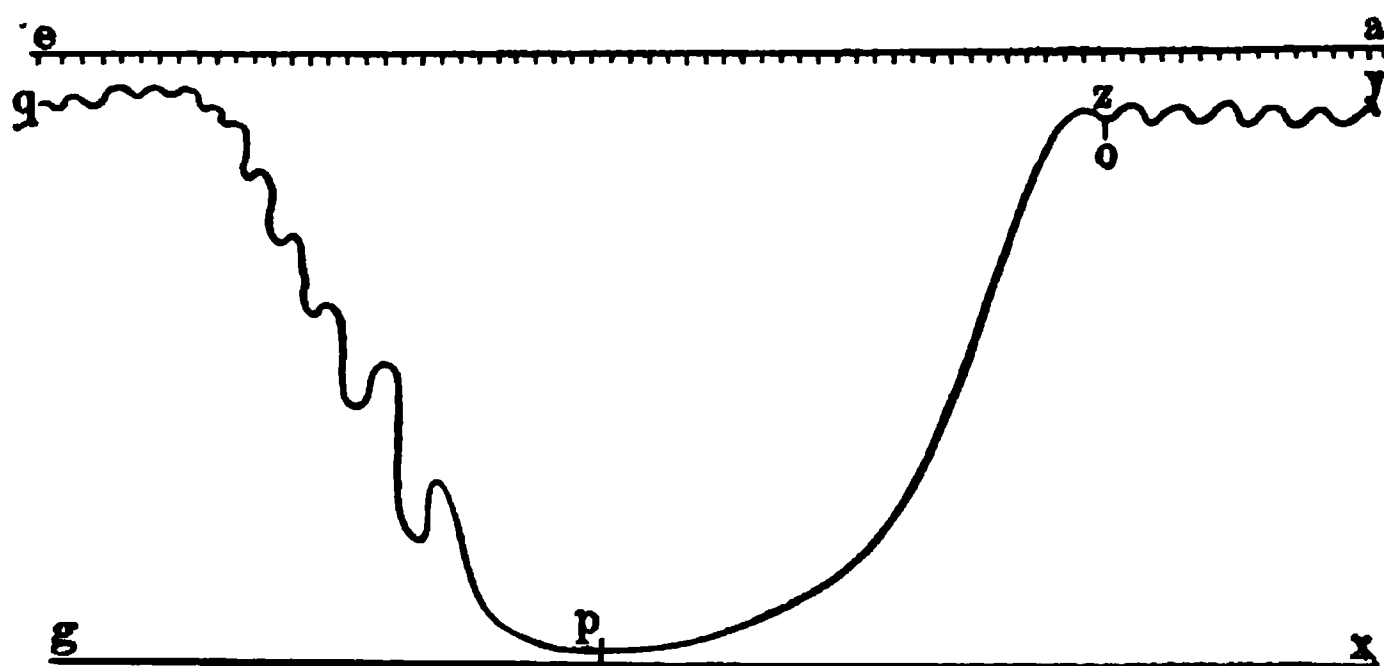

Fig. 102.—Tracing of arterial pressure during vagus inhibition of the heart. To be read from right to left: *yzµq*, blood pressure-line traced by the manometer pen; *o* indicates on the tracing the instant at which the nerve was stimulated; *p*, the instant at which the stimulation ended; *ae*, line traced by a pen marking half seconds; *xg*, line of no pressure, that is, level at which the pen would write were there no arterial pressure; the distance between it and the part of the manometer line directly above it multiplied by two gives the actual pressure in mercury in the artery at that moment. The small variations of pressure seen on the curve are due to beats of the heart; they are absent during the inhibition and slow for a short time after it.

surface, the small curves (*pulse-waves*) on which correspond to the slight increases of arterial pressure following each contraction of the left ventricle. The number of these small curves in a given time gives us therefore the pulse-rate. The pneumogastric is meanwhile exposed in the neck and cut across: the object of dividing it is to prevent stimuli travelling to the brain by the afferent fibres in it, as they would act on the nerve-centres and lead to complicated results. The peripheral end of the cut nerve is then stimulated, the excitation commencing at, say, the instant corresponding to the point *o* on the tracing.

It is seen that the heart does not stop at once but gives a beat or two and then stops as indicated by the sudden fall of arterial pressure and the absence of all pulse-waves from the tracing. If the stimulation be stopped at the instant indicated by *p*, the heart does not begin immediately to beat, but when it does, the beats are powerful and soon bring the arterial pressure back to its former level, or in many cases to a point above it for some time before the previous pressure and pulse-rate are regained. Such a tracing shows among other things that a certain "latent period" elapses before the stimulation of the inhibitory fibres influences the heart-beat, and that the influence of the stimulus once established continues a short time after the stimulation is stopped; and that the first beats after cessation of the inhibition are slow and powerful. Of course without any manometer one can detect the effect of cardio-inhibitory stimulus by a finger placed over the pulse of an animal or by listening to the heart-sounds, but the graphic method above described allows of much more accurate study.

It has been stated in a previous paragraph that stimulation of the cardiac nerve *usually* stops or slows the heart-beat of a frog. The reason for the qualifying term is that sometimes the stimulation quickens the beat. This is due to the fact that the nerve (see Fig. 99) is a mixed one and that the fibres it receives from the sympathetic are directly antagonistic in action to those derived from the vagus. In most cases when the whole trunk is stimulated the vagus fibres get the upper hand, but to be sure of pure cardio-inhibitory results the vagus must be stimulated before the sympathetic branch joins it. Then the action is always inhibitory; and certain other important phenomena may be observed, showing that the vagus contains fibres which tend to throw the heart into a better working state. When an exposed frog's heart is dying and has ceased to beat, or when the ventricle has come to rest though the sinus and auricles still work, it not unfrequently happens that a period of vagus stimulation is followed by a set of beats: or similarly that when the whole heart is beating feebly stimulation of the vagus is after a time followed by more forcible contractions. Hence it has been suggested that the nerve contains fibres which tend to promote the nutrition of the cardiac muscle, fibres which are anabolic and favor constructive chemical processes. Whether these fibres

are the same as the cardio-inhibitory or are a distinct set is still uncertain. In mammals, also, it is frequently noticeable that vagus inhibition of the heart is followed by a period of unusually powerful pulsation.

The Cardio-inhibitory Centre. This consists of nerve-cells lying in the medulla oblongata and giving origin to the cardio-inhibitory fibres. In some animals it seems to be normally always in a state of slight activity, sending out feeble impulses which exert a slight check on the rate of pulse. This is the case in the dog, for in that animal division of both pneumogastric nerves in the neck is followed by a quicker heart-beat: in the rabbit, on the other hand, the centre appears usually at rest, as section of the pneumogastrics in that animal has no effect on the pulse-rate. Whether normally in action or not the centre can readily be excited, especially by afferent impulses reaching it through abdominal nerves. If the intestines of a frog (the brain of which in front of the medulla oblongata has been entirely removed so as to make consciousness impossible) be exposed and sharply struck, the heart stops in diastole; but if both cardiac nerves have been previously divided this result does not follow. The stoppage is clearly then a reflex inhibition through the cardio-inhibitory centre and nerves, and the afferent tract can be readily traced. The afferent impulses from the intestine pass through the mesenteric branches of the sympathetic, for if these be cut no cardiac standstill follows the mechanical stimulation of the intestine, although the vagi be intact. If only the communicating branches from the sympathetic ganglia to the spinal cord be cut or only the anterior roots of the corresponding spinal nerves, or only the spinal cord above the place of entry of these roots, or only the medulla oblongata destroyed, yet, in each case, the intestinal stimulation causes no stoppage of the heart. When the standstill does result it is therefore reflex, the afferent path being—sensory nerve-endings in intestine, mesenteric nerves, sympathetic ganglion, communicating branches, anterior spinal roots, spinal cord to centre in medulla; the efferent fibres are the inhibitory in the vagus. The fainting which in man not infrequently follows a severe blow on the pit of the stomach is due to similar reflex excitation of the cardio-inhibitory centre: and the fainting seen during severe pain and that which certain odors cause in some persons are due to similar stimulation of

the cardio-inhibitory centre through sensory nerves, and serve to illustrate the many afferent fibres from different regions of the Body which can influence the heart-beat.

The cardio-inhibitory centre may also be stimulated directly (as by piercing it with a needle) and stop the heart. But a more interesting instance is its excitation by high arterial pressure. Nearly always a very high pressure in the aorta is accompanied by a slow pulse due to cardio-inhibitory nerve-impulses, for if the vagi be cut under such circumstances the heart-rate immediately increases. The slower beat, of course, by lessening the work of the heart tends to bring back the high arterial pressure to a more normal level, providing an adjustment of the heart's work to the condition of the arterial system at the time. The brain, enclosed in the rigid skull-cavity, is especially likely to be affected by increased arterial tension, for distension of the intra-cranial arteries must bring about greater pressure on all the other contents of the skull; and the cardio-inhibitory centre is very sensitive to increased pressure. If a small hole be bored through the skull of a dog and a little innocuous fluid injected so as to cause pressure on the brain, the beat of the heart is promptly slowed and weakened, but if the pneumogastrics have been previously cut the heart-beat is not influenced. In man similar stimulation of the cardio-inhibitory centre is shown in apoplexy, which is due to the bursting of some vessel inside the skull and the effusion of blood, which by pressure on the brain causes the unconsciousness and paralysis which characterize the stroke. During such a fit the pulse is almost invariably very slow from the action of the increased pressure on the cardio-inhibitory cells. This is clearly a preservative action, for the resulting lower arterial pressure makes the hæmorrhage less, and more likely to come to an end. Among conditions of the blood which stimulate the cardio-inhibitory apparatus may be mentioned deficient oxygenation, which will be referred to again when the phenomena of suffocation are described.

The Cardio-accelerator or Augmentor Nerves. The influence of these on the heart is to quicken or strengthen its beat or both: but only for a time, their final action being to hasten exhaustion; they are essentially katabolic in their influence on the nutrition of the organ.

Both in frog and mammal they pass to the heart from

the sympathetic, taking somewhat different paths in different animals. In the frog their course is shown in Fig. 99; in mammals most of them come from the upper thoracic ganglion of the sympathetic and the neighboring parts of the main sympathetic chain. If the heart of a frog be exposed and watched while the branch *s*, Fig. 99, is stimulated its beat is seen to be quickened, especially if the previous rate were slow: and quite similar phenomena may be observed when the corresponding nerves are stimulated in a rabbit or dog. And the beat is not merely made more rapid: it is distinctly more powerful for the time, the heart driving out more blood at each stroke (even though pressure in the aorta may be high) and thus doing increased work.

Though the augmentor fibres reach the heart through the sympathetic they have their centre (*cardio-accelerator centre*) in the medulla oblongata, from which in mammalia they pass down the spinal cord to the anterior roots of the upper thoracic spinal nerves, to the communicating branches, to the sympathetic ganglia, and thence to the cardiac plexus and the heart. Their centre, like the inhibitory, may be reflexly excited: powerful stimulation of a sensory nerve, after section of the vagi, usually quickens the pulse if the accelerator fibres passing from the thoracic ganglia be intact, but has no effect if these be previously divided. If the vagi are not cut the result is not so certain, as the afferent impulses may also excite the cardio-inhibitory centre and cause a mixed action: but speaking generally afferent impulses which in a conscious animal would cause acute but not extreme pain cause increase of the heart-beat. This by raising general arterial tension would for the time put the animal in good condition to make a vigorous effort, and so is obviously an unconscious adaptation of the organism for the preservation of its safety. While extreme pain or extensive injury involving many afferent nerves tends to cause fainting and loss of consciousness, the cardio-inhibitory centre getting the upper hand.

The Influence of Temperature Changes and of Calcium Salts on the Heart-beat. If the excised heart of a frog be cooled it beats more slowly; if heated, more quickly; until the temperature approaches the limit at which muscle passes into rigor. The observation is more difficult with mammals, but if the heart of a dog be completely separated from all the rest of the body except the lungs and supplied with blood

it is possible to keep it alive for some hours, beating regularly and powerfully, and on such a heart it is easy to observe that cooler blood causes slower beat and *vice versa.* While the quick pulse observed in fevers may therefore be in part due to paralysis of the cardio-inhibitory centre or stimulation of the cardio-accelerator, it is in part at least due solely to the hotter blood circulating through the coronary vessels. Whether the higher temperature in this case acts primarily on the nerve-cells of the heart or on the muscle is not known.

If circulation be kept up through a frog's heart by the perfusion method (Fig. 100), the organ may be kept beating for a very long time if the liquid supplied be blood or serum. If only dilute solution (0.75%) of sodium chloride be given, the beat continues for some time, but not so long as if no liquid be circulated; the salt apparently washes out something which the heart needs. The beat of such a "washed-out" heart may be restored by substituting milk or serum or de-fibrinated blood for the saline solution, or even by adding to the sodium chloride a very little of a soluble calcium salt. Serum, blood, and milk all contain calcium salts, and albuminous solutions free from calcium (as paraglobulin) do not restore the beat; nor do serum or milk or blood deprived of calcium. Hence the presence of some salt of that metal seems to have a close relation to the functional activity of the heart, as indeed it has to muscular activity in general.

CHAPTER XVIII.

THE VASO-MOTOR NERVES AND NERVE-CENTRES.

The Nerves of the Blood-vessels. The arteries, as already pointed out, possess a muscular coat composed of fibres arranged around them, so that their contraction can narrow the vessels. This coat is most prominent in the smaller vessels,—those of the size which go to supply separate organs,—but disappears again in the smallest branches, which are about to divide into capillaries for the individual tissue elements of an organ. These vascular muscles are under the control of certain special nerves called *vaso-motor*, and these latter can thus govern the amount of blood reaching any organ at a given time. Most of the vascular nerve-fibres have their origin in the cerebro-spinal centre, though they pass through sympathetic ganglia on their way to the vessels. In a few regions ganglion-cells are found lying close to the arteries, and some of the vaso-motor fibres are probably connected with them, but as a rule they end directly in the muscular coat.

In the heart we had to consider a rhythmically contracting organ the force of whose contractions could be increased or diminished by the influence of extrinsic nerves; in the arteries, speaking broadly, we have to deal with muscle in a condition of tonic or constant contraction, which contraction can be increased by impulses coming through excitor or *vaso-constrictor* nerves, and diminished through the activity of inhibitory or *vaso-dilator* nerves. The general tonic contraction of the arterial muscle is, however, much more dependent on the vaso-constrictor nerve-fibres than is the beat of the heart on the cardio-excitor nerves. The inhibitory set of vaso-motor nerves have a much less extensive distribution over the arterial system than the constrictor.

The Vaso-constrictor Nerves. If the ear of a white rabbit be held up against the light while the animal is kept quiet and not alarmed, the red central artery can be seen coursing

along the translucent organ, giving off branches which by subdivision become too small to be separately visible, and the whole ear has a pink color and is warm from the abundant blood flowing through it. Attentive observation will show also that the calibre of the main artery is not constant; at somewhat irregular periods of a minute or more it dilates and contracts a little.

If the sympathetic trunk have been previously divided on the other side of the neck of the animal, the ear on that side will present a very different appearance. It arteries will be much dilated and the whole ear fuller of blood, redder, and distinctly warmer; the slow alternating variations in arterial diameter also have disappeared. We get thus evidence that the normal mean calibre of the artery is maintained by influences reaching its muscular coat through the cervical sympathetic. Stimulation of the upper end of the cut nerve confirms this opinion. It is then seen that the arteries of the corresponding ear gradually contract until even the main vessel can hardly be seen, and in consequence the whole ear becomes pale and cold. After the stimulation is stopped the arteries again slowly dilate until they have regained their full paralytic size, and they usually remain permanently in that condition. Sometimes they regain after some days almost the size of those in the ear on the uninjured side, even when the nerve has not only been cut, but the upper cervical sympathetic ganglion extirpated; this seems to indicate that the arterial muscle has a small automaticity of its own tending to keep it in a moderate state of contraction, but it is less marked than the automaticity of the myocardium.

Quite similar phenomena can be observed in transparent parts of other living animals, as in the web of a frog's foot, the arteries of which dilate after section of the sciatic nerve and constrict when the peripheral end of the nerve is stimulated. In the case of other parts changes in temperature may be used to detect alterations in the flow of blood. In a dog or cat, for example, a sensitive thermometer placed between the toes indicates a rise of temperature, owing to increased flow of warm blood through the skin, after section of the chief nerve of the limb, and a fall of temperature (usually) during stimulation of the peripheral end of the divided nerve.

When the vaso-constrictor nerves cut are those controlling a

large number of arteries, the dilatation of the latter so much diminishes peripheral resistance to the blood-flow as to lead to a marked fall of general arterial pressure; and, due care being taken to avoid or to allow for concomitant variations in the rate or force of the heart's beat, this gives us another useful method of studying the distribution of the nerves concerned. For example, the *splanchnic nerves* are branches which spring from the thoracic portion of the sympathetic chain and pass through the diaphragm to end in the gangliated *solar plexus* from which nerves pass to the arteries of most of the abdominal viscera. When the splanchnic nerves are cut on both sides arterial pressure falls enormously, from say 120 millimetres of mercury in the carotid of a dog to 15 or 20 millimetres, most of the blood of the body lying almost stagnant in the dilated blood-vessels of the abdomen. On the other hand, stimulation of the splanchnic nerves so diminishes the paths open for the circulation of the blood as to enormously increase general blood-pressure; especially if the cardio-inhibitory nerves be first divided so that raised blood-pressure inside the skull-chamber may not slow the heart-beat.

The skin and the abdominal organs seem to be the predominant localities of distribution of the vaso-constrictor nerves: other parts have them, but not in quantity sufficient to bring about any great general change in the blood-flow. In the abdomen is warmer, in the skin cooler blood: and according to the amount of heat produced in the Body and the temperature of the surrounding medium, the vessels of abdomen and skin contract or relax so as to control the proportion of blood sent to the skin to lose heat.

The Vaso-constrictor Centre. The constrictor nerves of the arteries do not originate in the sympathetic system. If all the branches of the latter be left intact, the phenomena of paralytic dilatation of the blood-vessels can be fully brought about by dividing the communicating branches between certain spinal nerves and the corresponding sympathetic ganglia, or by dividing the anterior roots of certain spinal nerves. In this way it can be shown that the fibres all proceed from the thoracic and lumbar regions of the spinal cord, but have not their origin in the cord. If it be cut anywhere in the cervical region, all arteries having a constrictor nerve supply are paralyzed, while stimulation of the posterior end

of the divided cord causes widespread arterial constriction. The main centre for the vaso-constrictors must then lie as far forward as the medulla: and as all the brain in front of the medulla oblongata can be removed without any consequent arterial paralysis, the centre must lie in the medulla itself. This centre is often named the *vaso-motor centre*, but it is better to distinguish it as the *vaso-constrictor* from the centre for the dilator efferent nerves.

The Control of the Vaso-constrictor Centre. The vaso-constrictor centre is automatic; it maintains a certain amount of activity of its own, independently of any stimuli reaching it through afferent nerve-fibres. Nevertheless, like nearly all automatic nerve-centres, it is under reflex control, so that its activity may be increased or lessened by afferent impulses conveyed to it. Nearly every sensory nerve of the Body is in connection with it; any stimulus giving rise to pain, for example, excites it, and thus constricting the arteries, increases the peripheral resistance to the blood-flow and raises arterial pressure. On the other hand, certain fibres conveying impulses from the heart inhibit the centre and dilate the arteries, lower blood-pressure, and diminish the resistance to be overcome by the heart. These afferent fibres, which have been already referred to as the large medullated fibres (p. 263) of the pneumogastric, are known as the *depressor fibres*, or in certain animals, for example the rabbit, where they are all collected into one branch, as the *depressor nerve*. If this nerve be divided and its cardiac end stimulated no effect is produced, but if its central end (that still connected with the rest of the pneumogastric trunk and through it with the medulla oblongata) be stimulated, arterial pressure gradually falls; this result being dependent upon a dilatation of the small arteries, and consequent diminution of the peripheral resistance, following an inhibition of the vaso-constrictor centre brought about by the depressor nerve. Through the depressor nerve the heart can therefore influence the calibre of the small arteries and, by lowering aortic pressure, diminish its own work if need be. In Fig. 103 is reproduced a tracing of the great but slow fall of blood-pressure which results from stimulation of the depressor fibres. It shows the slow fall of pressure and slightly changed pulse-rate accompanying the slow dilatation of the arteries, and may be compared with the rapid fall and slow pulse brought about (Fig. 102) by excita-

tion of the cardio-inhibitory nerves. The latent period is also noticeably long and the effect of the stimulus outlasts considerably the time of its application.

Blushing. The depressor nerves control a great part of the vaso-constrictor centre (especially that portion of it connected with the splanchnic nerves) and so can bring about dilatation of a large number of arteries—their influence is accordingly called into play when general arterial pressure is to be lowered, but is useless for controlling local blood-supply. This is managed in part by other afferent nerves, each of which inhibits a small part only of the vaso-constrictor centre, governing the arteries of a limited tract of the Body; the dilata-
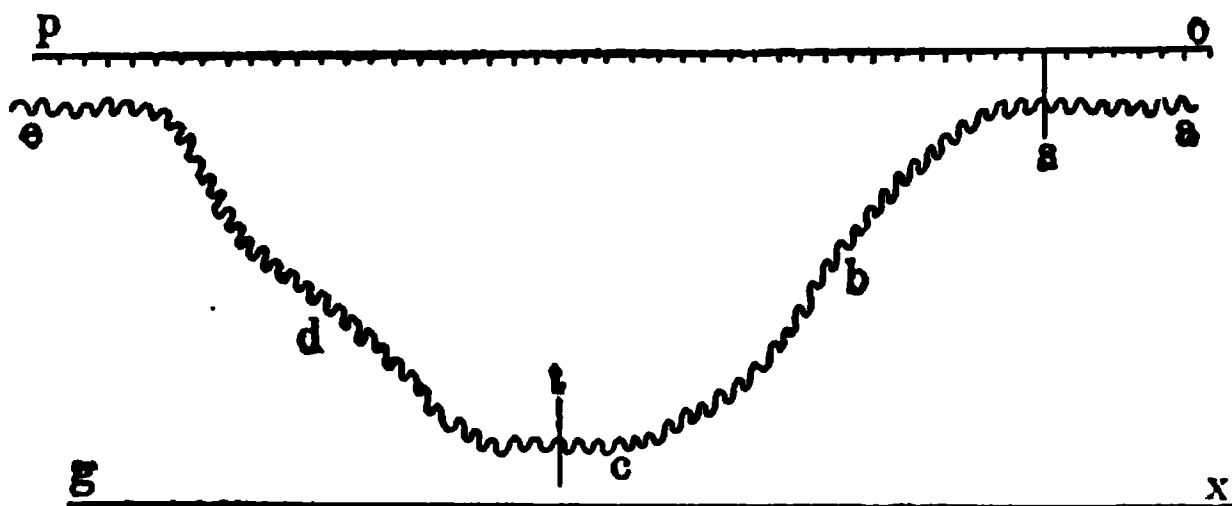
Fig. 103.—Tracing of pressure from femoral artery of a rabbit showing the influence of stimulation of the central end of the depressor nerve; to be read from right to left: *a b c d e*, tracing of arterial pressure, the small variations indicating heartbeats; *op*, tracing of seconds pen; *s*, moment of commencement of stimulation; *t*, cessation of stimulation; *xg*, line of no pressure.

tion of these increases the amount of blood flowing through the particular region to which they are distributed, but does not affect the total resistance to the blood-flow sufficiently to influence noticeably the general pressure in the arterial system. In blushing, for example under the influence of an emotion, that part of the vaso-motor centre which supplies constrictor nerves to the arteries of the skin of the neck and face, is inhibited by nerve-fibres proceeding from the cerebrum to the medulla oblongata, and the face and neck consequently become full of blood and flush up. Quite similar phenomena occur under other conditions in many parts of the Body, although when not visible on the surface we do not usually call them blushes. The mucous membrane lining the empty stomach is pallid and its arteries contracted, but as soon as food enters the organ it becomes red and full of blood; the food stimulating afferent nerve-fibres there, which inhibit

that part of the vaso-motor centre which governs the gastric arteries.

Taking Cold. This common disease is not unfrequently caused through undue reflex excitement of the vaso-motor centre. Cold acting upon the skin stimulates, through the afferent nerves, the portion of the vaso-motor centre governing the skin arteries, and the latter become contracted, as shown by the pallor of the surface. This has a twofold influence— in the first place, more blood is thrown into internal parts, and in the second, contraction of the arteries over so much of the Body considerably raises the general blood-pressure. Consequently the vessels of internal parts become overgorged or "congested," a condition which readily passes into inflammation. The action is of course primarily protective, to prevent too great loss of heat from the Body; but if internal organs be weak or diseased or if the exposure to wet or cold be prolonged, it is apt to be followed by catarrh or inflammation of more or less of the respiratory tract causing bronchitis, or of the intestines causing diarrhœa. In fact the common summer diarrhœa is far more often due to a chill of the surface, causing intestinal catarrh, than to the fruits eaten in that season which are so often blamed for it. The best preventative is to wear, when exposed to great changes of temperature, a woollen or at least a cotton garment over the trunk of the Body; linen is so good a conductor of heat that it permits any change in the external temperature to act almost at once upon the surface of the Body. After an unavoidable exposure to cold or wet the thing to be done is of course to restore the cutaneous circulation; for this purpose movement should be persisted in, and a thick dry outer covering put on, until warm and dry underclothing can be obtained.

For healthy persons a temporary exposure to cold, as a plunge in a bath, is good, since in them the sudden contraction of the cutaneous arteries soon passes off and is succeeded by a dilatation causing a warm healthy glow on the surface. If the bather remain too long in cold water, however, this reaction passes off and is succeeded by a more persistent chilliness of the surface, which may even last all day. The bath should therefore be left before this occurs, but no absolute time can be stated, as the reaction is more marked and lasts longer in strong persons, and in those used to cold bathing, than in others.

Vaso-dilator Nerves. We have already noticed, in the case of the stomach, one method by which a locally increased blood-supply may be brought about in an organ while it is at work, viz., by inhibition of local vaso-constrictor fibres. Frequently, however, in the Body this is managed in another way; by efferent vaso-dilator nerves which inhibit or paralyze, not the vaso-constrictor centre, but the muscles of the blood-vessels directly. The nerves of the skeletal muscles for example contain two sets of efferent fibres: one motor proper and the other vaso-dilator. When the muscle contracts in a reflex action or under the influence of the will both sets of fibres are excited; so that when the organ is set at work its arteries are simultaneously dilated and more blood flows through it. But if the animal have previously administered to it such a dose of curare as to just paralyze the true motor-fibres, stimulation of the nerve produces dilatation of the arteries without a corresponding muscular contraction. Quite a similar thing occurs in the salivary glands. Their cells, which form the saliva, are aroused to activity by special nerve-fibres; but the gland-nerve also contains a quite distinct set of vaso-dilator fibres which normally cause a simultaneous dilatation of the gland-artery, though either can be artificially stimulated by itself and produce its effect alone. Through such arrangements the distribution of the blood in the Body at any moment is governed: so that working parts shall have abundance and other parts less, while at the same time the general arterial pressure remains the same on the average; since the expansion of a few small local branches but little influences the total peripheral resistance in the vascular system. Moreover, commonly when one set of organs is at work with its vessels dilated, others are at rest with their arteries comparatively contracted, and so a general average blood-pressure is maintained. Few persons, for example, feel inclined to do brain-work after a heavy meal: for then a great part of the blood of the whole Body is led off into the dilated vessels of the digestive organs, and the brain gets a smaller supply. On the other hand, when the brain is at work its vessels are dilated and often the whole head flushed: and so excitement or hard thought after a meal is very apt to produce an attack of indigestion, by diverting the blood from the abdominal organs, where it ought to be at that time. Young persons, whose organs have a superabun-

dance of energy enabling them to work under unfavorable conditions, are less apt to suffer in such ways than their elders. One sees boys running actively about after eating, when older people feel a desire to sit quiet and ruminate—or even to go to sleep.

When the nerve of a limb is cut and its peripheral end is stimulated the usual result is arterial constriction, because the constrictor fibres are more numerous and more powerful than the dilator; a day or two after section, when the nerve has begun to degenerate, stimulation, however, causes dilatation, apparently because the constrictor fibres degenerate more quickly: and when the stimuli (as induction shocks) given to the nerve are repeated at only a slow rate the dilator effect frequently overcomes the constrictor.

The Vaso-dilator Centre. The vaso-dilator nerves, like the vaso-constrictor, seem to originate primarily in a centre in the medulla oblongata. In regard to the arteries in general, they play a much less conspicuous part than their analogues, the cardio-inhibitory fibres, do in regard to the heart.

The Vaso-motor Nerves of the Veins. Most veins have a muscular coat, though it is much less developed than in the arteries, and this coat is probably under the control of nerve-fibres. Satisfactory evidence of their existence is still wanting.

The Vascular Phenomena of Inflammation. When some transparent portion of an animal (for example the mesentery of a mouse or guinea-pig) is carefully exposed and studied with a microscope, the normal flow in the small vessels may be studied for some time, much as in the web of the frog. If an irritant be applied, the immediate result is a widening of the small arteries and a greater and more rapid flow through them and the capillaries and veins. This seems dependent mainly on a direct paralysis of the arteries, and if the irritant be transient in its influence the *congested* condition soon passes off. If the irritant be more powerful, the vascular dilatation continues and other circulatory changes are seen. The corpuscles, instead of keeping, as is usual in arteries of microscope size, to the central part of the tube (*axial current*), spread more evenly, and the white corpuscles especially tend to pass into the layer of liquid in immediate contact with the inner coat of the artery, and at the same time to exhibit much more marked amœboid move-

ments than they commonly do while travelling in the blood-current. The platelets, also, which are normally confined to the axial currents, now pass towards the sides. If this stage of very early *inflammation* pass on to the next, it is observed that white corpuscles and platelets both stick to the inside of the vessels. The platelets next adhere together and break down into granular masses, and the white corpuscles thrust amœboid processes between the lining-cells of the capillaries and smallest veins, and begin to push their way through. By these means a considerable impediment to the blood-flow is caused, and the circulation becomes slower, though all the vessels of the part may be dilated. If the inflammation continue, many white corpuscles pass quite out of the vessels (*migration*) and enter the neighboring lymph-spaces: the red corpuscles get blocked and squeezed together into a mass in which their individual boundaries are indistinguishable, and some of them may even be squeezed through the walls of the capillaries (*diapedesis*). Next all blood-flow in the area under observation may be stopped, while more lymph than normal collects in it. From this state recovery may take place; or continued inflammation may lead to destruction of the part. The primary local disturbances in the circulation seem due to changes in the inner coats of the vessels of the irritated region; but an extensive continued inflammation produces fever and many other secondary general results, partly through the absorption of disease products from the inflamed part and partly through irritation of afferent nerve-fibres which throw various nerve-centres into abnormal action.

CHAPTER XIX.

THE SECRETORY TISSUES AND ORGANS.

Definitions. In its broad etymological meaning a secretion is any substance separated or derived from the blood, so that in a certain sense all the solid tissues of the Body, built up from materials supplied by the blood, are secretions. In practice the name has a more limited application and is given to two classes of substances, distinguished as true or *external secretions* and *internal secretions.*

Internal secretions are the results of the vital activities of various organs, their by-products, passed out directly into the lymph and blood; and in many cases are simple wastes, sent to the blood-stream for conveyance to other organs which get rid of them: such, for example, is the carbon dioxide formed in every part of the Body. In other cases the by-products of certain organs, after absorption into the blood, have to be further changed in a second organ before elimination, and are probably of use to this second—a part of its pabulum: as an instance we may take leucin (amido-caproic acid), which is formed in many organs and, given by them to the blood, is carried to the liver, the cells of which convert it (or at least a great part of it) into urea, to be subsequently eliminated by the kidneys. A third very important class of internal secretions consists of substances formed only in one organ or one pair of organs and yielded by them to the blood which flows through them, the presence of which substances in the blood is essential to the healthy nutrition and the continuance of the life of the Body: in such cases removal or extensive disease of the producing organ results in death. Examples are to be found in substances which the thyroid body and suprarenal capsules produce; they will be considered more fully in Chapter XXIII.

Excluding such things as cast hairs and epidermic scales, the true or external secretions may be defined as gases or liquids, often of very complex composition, passed out on

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some free surface of the Body, either that of the general exterior or of some internal cavity, or into recesses communicating with such a surface. The true secretions fall into two classes: one in which the product is of no further use in the Body and is merely separated for removal, as the urine; and one in which the product is intended to be used, for instance as a solvent in the digestion of food. The former group are sometimes distinguished as *excretions* and the latter as *secretion.s proper*, but there is no real difference between them, the organs and processes concerned being fundamentally alike in each case. A better division is into *transudata* and *secretions,* a transudation being a product which contains nothing which did not previously exist in the blood, and only in such quantity as might be derivable from it by merely physical processes; while a secretion in addition to transudation elements contains a *specific element,* due to the special physiological activity of the secretory organ; being either something which does not exist in the blood at all or something which, existing in the blood in small quantity, exists in the secretion in such a high proportion that it must have been actively picked up and conveyed there by the secretory tissues concerned. For instance, the gastric juice contains free hydrochloric acid which does not exist in the blood; and the urine contains so much urea that we must suppose the kidney-cells to have a peculiar power of removing that body from the liquids flowing near them. This subdivision is also justifiable on histological grounds; wherever there is a secreting surface or recess it is lined by cells, but these cells where transudata are formed (as on the serous membranes) are mere flat scales, with little or no protoplasm remaining in them (Fig. 11B), while the cells which line a true secreting organ are cuboidal, spherical, or columnar, and still retain, with their high physiological activity, a good deal of their primitive protoplasm.

Organs of Secretion. The simplest form in which a secreting organ occurs (*A*, Fig. 104) is that of a flat membrane provided with a layer of cells, *a*, on one side (that on which the secretion is poured out) and with a network of capillary blood-vessels, *c*, on the other. The dividing membrane, *b*, is known as the *basement membrane* and is usually made up of flat, closely fitting connective-tissue corpuscles; supporting it on its deep side is a layer of connective tissue, *d*, in which the blood-vessels and lymphatics are supported. Such simple forms

of secreting surfaces are found on the serous membranes, but are not common; in most cases an extended area is required to form the necessary amount of secretion, and if this were attained simply by spreading out plane surfaces, these from their number and extent would be hard to pack conveniently in the Body. Accordingly in most cases, the greater area is attained by folding the secreting surface in various ways so that a large area can be packed in a small bulk, just as a Chinese lantern when shut up occupies much less space than when extended, although its actual surface remains of the same extent. In a few cases the folding takes the form of protrusions into the cavity of the secreting organ as indicated at *C*, Fig. 104, and found on some synovial membranes; but much more commonly the surface extension is attained in another way, the basement membrane, covered by its epithelium, being pitted in or involuted as at *B*. Such a secreting organ is known as a gland.

Forms of Glands. In some cases the surface involutions are uniform in diameter, or nearly so, throughout (*B*, Fig. 104). Such glands are known as *tubular;* examples are found in the lining coat of the stomach (Fig. 113); also in the skin (Fig. 135), where they form the *sweat-glands.* In other cases the involution swells out at its deeper end and becomes more or less sacculated (*E*); such glands are *racemose* or *acinous.* The small glands which form the oily matter poured out on the hairs are of this type. In both kinds the lining cells near the deeper end are commonly different in character from the rest; and around that part of the gland the blood-vessels form a closer network. These deeper cells form the true secreting elements of the gland, and the passage, lined with different cells, leading from them to the surface, and serving merely to carry off the secretion, is known as the *gland-duct.* When the duct is undivided the gland is *simple;* but when, as is more usual, it is branched and each branch has a true secreting part at its end, we get a compound gland, tubular (*G*) or racemose (*F, H*) as the case may be. In such cases the main duct, into which the rest open, is often of considerable length, so that the secretion is poured out at some distance from the main mass of the gland.

A fully formed gland, *H*, thus comes to be a complex structure, consisting primarily of a duct, *c*, ductules, *dd*, and secreting recesses, *ee*. The ducts and ductules are lined with

epithelium which is merely protective and differs in charac-
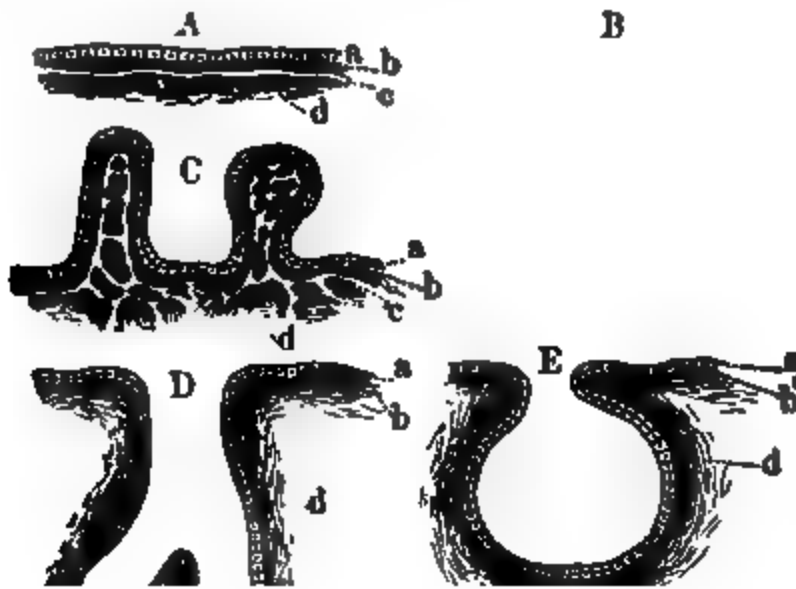ter from the secreting epithelium which lines the deepest

Fig. 104.—Forms of glands. *A.* a simple secreting surface ; *a.* its epithelium ;
b, basement membrane ; *c,* capillaries . *B.* a simple tubular gland ; *C.* a secreting
surface increased by protrusions ; *E.* a simple racemose gland ; *D* and *G.* com-
pound tubular glands ; *F,* a compound racemose gland   In all but *A, B,* and *C*
the capillaries are omitted for the sake of clearness.   *H,* half of a highly developed
racemose gland ; *c,* its main duct.

parts.   Surrounding each subdivision and binding it to its
neighbors is the *gland stroma* formed of connective tissue, a

layer of which also commonly envelops the whole gland, as its *capsule*. Usually on looking at the surface of a large gland it is seen to be separated by partitions of its stroma, coarser than the rest, into *lobes*, each of which answers to a main division of the primary duct; and the lobes are often similarly divided into smaller parts or *lobules*. In the connective tissue between the lobes and lobules blood-vessels penetrate, to end in fine capillary vessels around the terminal recesses. They never penetrate the basement membrane. Lymphatics and nerves take a similar course; there is reason to believe that the nerve-fibres penetrate the basement membrane and become directly united with the secreting cells of some glands.

The Physical Processes in Secretion. From the structure of a gland it is clear that all matters derived from the blood and poured into its cavity must pass not only through the walls of the capillary blood-vessels, but also, by filtration or dialysis, through the basement membrane and the lining epithelium. By filtration is meant the passage of a fluid under pressure through the coarser mechanical pores of a membrane, as in the ordinary filtering processes of a chemical laboratory ; and the higher the pressure on the liquid to be filtered the greater the amount which, other things being equal, will pass through in a given time. Since in the living Body the liquid pressure in the blood-capillaries is nearly always higher than that outside them, filtration is apt to take place everywhere to a greater or less extent, and will be increased in amount in any region by circumstances raising blood-pressure there, and diminished by those lowering it. To a certain extent also the nature of the liquid filtered has an influence. True solutions, as those of salt in water, passed through unchanged ; but solutions containing substances such as boiled starch or raw egg-albumen, which swell up greatly in water rather than truly dissolve, are altered by filtration ; the filtrate containing less of the imperfectly dissolved body than the unfiltered liquid. The higher the pressure the greater the proportion of such substances which gets through ; and if the pressure is slight the water or other solvent may alone pass, leaving all the rest behind on the filter. Under moderate pressure the blood may thus lose by filtration only such bodies as water and salines ; while an increase of arterial pressure may lead to

the passage of albumen and fibrinogen. Under healthy conditions, for example, the urine contains no albumen, but anything considerably increasing the capillary pressure in the kidneys will cause it to appear. *Dialysis* or *osmosis* has already been considered (p. 42); by it substances pass through the intermolecular pores of a membrane independently of the pressure on either side, and for its occurrence two liquids of different chemical constitution are required, one on each side of the membrane. At least if diffusion takes place, as is probable, between two exactly similar solutions, the amount and character of the substances passing opposite ways in a given time are exactly equal, so that no change is produced by the dialysis; which practically amounts to the same thing as if none occurred. When a solution is placed on one side of a membrane allowing of dialysis, and pure water on the other, it is found that for every molecule of the dissolved body that passes one way a definite amount of water, called the *endosmotic equivalent* of that body, passes in the opposite direction. Crystalline bodies as a rule (hæmoglobin is an exception) have a low endosmotic equivalent or are readily dialyzable; while *colloids*, such as gum and proteids, have a very high one, so that to get, by dialysis, a small amount of albumen through a membrane, a practically infinite amount of water must pass the other way. Accordingly, if we find such bodies in a secretion we cannot suppose that they have been derived from the blood by mere osmosis.

The Chemical Processes of Secretion. As above pointed out certain secretions, called transudata, seem to be products of filtration and dialysis alone, containing only such substances as those which are found in the blood-plasma, more or less altered in relative quantity by the ease or difficulty with which they severally passed through the layers met with on their way to the surface. But in many cases the composition of a secretion cannot be accounted for in this way ; it contains some *specific element*, either a substance which does not exist in the blood at all and must therefore have been added by the secreting membrane, or some body which, although existing in the blood, does so in such minute proportion, compared with that in which it is found in the secretion, that some special activity of the secreting cells is indicated: some affinity in them for these bodies by which they actively pick them up.

Each living cell, we have seen, is the seat of constant chemical activity, taking up materials from the medium about it, transforming and utilizing them, and sooner or later restoring their elements, differently combined, to the outer medium. By such means it builds up and maintains its living substance, and obtains energy to carry on its daily work. While this is true of all cells in the Body, we find certain groups in which chemical metabolism is the prominent fact—cells which are specialized for this purpose just as muscular fibre is for contraction or nerve-fibre for conduction; and certain of these prominently *metabolic tissues* exist in the true glands and produce or collect the specific elements of their secretions. Their chemical processes are no doubt primarily directed to their own nutritive maintenance; they live primarily for themselves, but their nutritive processes are such that the bodies formed in them and sent into the secretion are such as to be useful to the rest of the cells of the community; or the bodies which they specially collect, and in a certain sense feed on, are those the removal of which from the blood is essential for the general good. Their individual nutritive peculiarities are utilized for the welfare of the whole Body.

The Mode of Activity of Secretory Cells. If we consider the modes of activity of living cells in general, it becomes clear that secretory cells may produce the specific element of a secretion in either of two ways. They may, as a by-result of their living play of forces, produce chemical changes in the surrounding medium ; or they may build up certain substances in themselves and then set them free as specific elements. Yeast, for example, in a saccharine solution causes the rearrangement into carbon dioxide, alcohol, glycerine and succinic acid, of many atoms of carbon, hydrogen and oxygen which previously existed as sugar; and a very considerable quantity of sugar may be broken up by the activity of a few living yeast-cells. How the latter act we do not know with certainty, but most likely by picking certain atoms out of the sugar molecule, and leaving the rest to fall down into simpler compounds. On the other hand, we find cells which form and store up in themselves large quantities of substances, which they afterwards liberate; starch, for instance, being formed and laid by in many fruit-cells, and

afterwards dissolved and sent in solution to nourish the young plant.

Gland-cells might *a priori* give rise to the specific elements of secretions in either of these ways, and we have to seek in which manner they work. Do they simply act as ferments (however that is) upon the surrounding medium; or do they form or collect the bodies characterizing their secretion, first within their own substance, and then liberate them, either disintegrating or not at the same time? At present there is a large and an increasing mass of evidence in favor of the second view. There is, no doubt, some reason to believe that every living cell can act more or less as a ferment upon certain solutions should they come into contact with it. Not always, of course, as an alcoholic ferment, though even as regards that one fermentative power it seems very generally possessed by vegetable cells, and there is some evidence that alcohol is normally produced in small amount (and presumably by the fermentation of sugar) under the influence of certain of the living tissues of the Human Body. As regards distinctively secretory cells, however, the evidence is all the other way, and in many cases we can see the specific element collecting in the gland-cells before it is set free in the secretion. For example, in the oil-glands of the skin (Chapter XXVIII) we find the secreting cells, at first granular, nucleated, and protoplasmic, gradually undergoing changes by which their protoplasm disappears and is replaced by oil-droplets, until finally the whole cell falls to bits and its detritus forms the secretion; the cells being replaced by new ones constantly formed within the gland. In such cases the secretion is the ultimate product of the cell-life, the result of degenerative changes of old age occurring in it.

In other cases, however, the liberation of the specific element is not attended with the destruction of the secreting cell; as an example we may take the pancreas, which is a large gland lying in the abdomen and forming a secretion used in digestion. Among others, this secretion possesses the power, under certain conditions, of dissolving proteids and converting them into dialyzable peptones (p. 10). This it owes to a specific element known as *trypsin*, the formation of which, or rather of its forerunner *trypsinogen*, within the gland-cells can be traced with the microscope.

The pancreas, like the majority of the glands connected with the alimentary canal, has an intermittent activity, determined by the presence or absence of food in various parts of the digestive tract. If the organ be taken from a recently killed dog which has fasted thirty hours and, after proper preparation, be stained with carmine and examined microscopically, we get specimens of what we may call the " resting gland "—a gland which has not been secreting for some time. In these it will be seen that the cells lining the secreting recesses present two very distinct zones: an outer, next the basement membrane which combines with the coloring matter and is not granular, and an inner which is granular and does not pick up the carmine. The granules we shall find to be indications of the presence of a trypsin-yielding substance formed in the cells.

If another dog be kept fasting until it has a good appetite and be then allowed to eat as much meat as it will, the animal will commonly take so much that the stomach will only be emptied at the end of about twenty hours. This period may, so far as the pancreas is concerned, be divided into two. From the time the food enters the stomach and on for about ten hours, the gland secretes abundantly; after that the secretion dwindles, and by the end of the second ten hours has nearly ceased. We have, then, a time during which the pancreas is working hard, followed by a period in which its activity is very little, but during which it is abundantly supplied with food-materials. The pancreas taken from an animal at the end of the first period and prepared for microscopic examination will be found different from that taken from a dog killed at the end of the second digestion period, and also from the resting gland. Towards the end of the period of active work the gland-cells are diminished in size and the proportions of the granular and non-granular zones are quite altered. The latter now occupies most of the cell, while the granular non-staining inner zone is greatly diminished. During the secretion there is, therefore, a growth of the non-granular and a destruction of the granular zone; and the latter process rather exceeding the former, the whole secreting cell is diminished in size. During the second digestive period, when secretion is languid, exactly a reverse process takes place. The cells increase in size so as to become larger than those of the resting gland; and this growth is almost.

entirely due to the granular zone which now occupies most of the cell.

These facts suggest that during secretion the granular part of the cells is used up: but that, simultaneously, the deeper non-granular zone, being formed from materials yielded by the blood, gradually renews the granular. During active secretion the breaking down of the latter to yield the specific element occurs faster than its regeneration; in a later period, however, when the secretion is ceasing, the whole cell grows and, especially, the granular zone is formed faster than it is disintegrated; hence the great increase of that part of the cell. If this be so, then we ought to find some relationship between the digestive activity of an infusion or extract of the gland and the size of the granular zones of the cells; and it has been shown that such exists; the quantity of trypsin which can be obtained from a pancreas being proportionate to the size of that portion of its cells.

The trypsin, however, does not exist in the cells ready formed, but only a body which yields it under certain circumstances, and called *trypsinogen*.

If a perfectly fresh pancreas be divided into halves and one portion immediately minced and extracted with glycerine, while the other is laid aside for twenty-four hours in a warm place and then similarly treated, it will be found that the first glycerine extract has no power of digesting proteids, while the second is very active. In other words, the fresh gland does not contain trypsin, but only something which yields it under some conditions; among others, on being kept. The inactive glycerine extract of the fresh gland is, however, rich in trypsinogen: for if a little acetic acid be added to it, trypsin is formed and the extract becomes powerfully digestive.

We may, then, sum up the life of a pancreas-cell in this way. It grows by materials derived from the blood and first laid down in the non-granular zone. This latter, in the ordinary course of the cell-life, gives rise to the granular zone; and in this is a store of trypsinogen produced by the active metabolisms of the cell. When the gland secretes, the trypsinogen is converted into trypsin and set free in the secretion; but in the resting gland this transformation does not occur. During secretory activity, therefore, the chemical

processes taking place in the cell are different from those at other periods; and we have next to consider how this change in the mode of life of the cells is brought about.

Influence of the Nervous System upon Secretion. When the gland is active it is fuller of blood than when at rest: its arteries are dilated and its capillaries gorged so that it gets a brighter pink color; this extra blood-supply might be the primary cause of the altered metabolism. Again, the activity of the pancreas is under the influence of the nervous system, as proved not only by the reflex secretion called forth when food enters the stomach, but also by the fact that electrical stimulation of the medulla oblongata will cause the gland to secrete. The nervous system may, however, only act through the nerves governing the calibre of the gland arteries, and so but indirectly on the secreting cells; while on the other hand it is possible that nerve-fibres act directly upon the gland-cells and, controlling their nutritive processes, govern the production of the trypsin. To decide between the relative importance of these possible agencies we must pass to the consideration of other glands; since the question can only be decided by experiment upon the lower animals, and the position of the pancreas and the difficulty of getting at its nerves without such severe operations as upset the physiological condition of the animal furnish obstacles to its study which have not yet been overcome.

In certain other glands, however, we find conclusive evidence of a direct action of nerve-fibres upon the secreting elements. When the sciatic nerve of a cat is stimulated electrically, the balls of its feet sweat. Under ordinary circumstances they become at the same time red and full of blood; but that this congestion is a factor of subsidiary importance as regards secretion is proved by the facts that stimulation of the nerve is still able to excite the gland-cells and cause sweating in a limb which has been amputated ten or fifteen minutes (and in which therefore no circulatory changes can occur) and also by the cold sweats, with a pallid skin, of phthisis and the death-agony. It is, however, with reference to the submaxillary and parotid salivary glands that our information is most precise.

When the mouth is empty and the jaws at rest the salivary secretion is comparatively little: but a sapid substance placed on the tongue will cause a copious flow. The phe-

nomenon is closely comparable to the production of a reflex muscular contraction. A stimulus acting upon an irritable tissue excites through it certain afferent nerve-fibres; these excite a nerve-centre, which in turn stimulates efferent fibres; going to a muscle in the one case, to a gland in the other. It will be useful to consider again for a moment what occurs in the case of the muscle, taking account only of the efferent fibres and the parts they act upon.

When a muscle in the Body is made to contract reflexly, through its nerve, two events occur in it. One is the shortening of the muscular fibres; the other is the dilatation of the muscular arteries; every muscular nerve contains two sets of fibres, one motor and one vaso-dilator, and normally both act together. In this case, however, it is clear that the activities of both, though correlated, are essentially independent. The contraction is not due to the greater blood-flow, for not only can an excised muscle entirely deprived of blood be made to contract by stimulating its nerves, but in an animal to which a small dose of curari—the arrow-poison of certain South American Indians—has been given, stimulation of the nerve will cause the vascular dilatation but no muscular contraction: the curari paralyzing the motor fibres, but, unless in large doses, leaving the vaso-dilators intact. The muscular fibres themselves are unacted upon by the poison, as is proved by their ready contraction when directly stimulated by an electric shock.

Now let us return to the salivary glands and see how far the facts are comparable. The main nerve of the submaxillary gland is known as the *chorda tympani.* If it be divided in a narcotized dog, and a tube placed in the gland-duct, no saliva will flow. But on stimulating the peripheral end of the nerve (that end still connected with the gland) an abundant secretion takes place. At the same time there is a great dilatation of the arteries of the organ, much more blood than before flowing through it in a given time: the *chorda* obviously then contains vaso-dilator fibres. Now in this case it might very well be that the process was different from that in a muscle. It is conceivable that the secretion may be but a filtration due to increased pressure in the gland capillaries, consequent on dilatation of the arteries supplying them. If a greater filtration into the lymph spaces of the gland took place, this liquid might then merely ooze on

through the secreting cells into the commencing ducts and, as it passed through, dissolve out and carry on from the cells the specific organic elements of the secretion. Of these, in the submaxillary of the dog at least, mucin is the most important and abundant. That, however, the process is quite different, and that there are in the gland true secretory fibres in addition to the vaso-dilator, just as in the muscle there are true motor fibres, is proved by other experiments.

If the flow of liquid from the excited gland were merely the outcome of a filtration dependent on increased blood-pressure in it, then it is clear that the pressure of the secretion in the duct could never rise above the pressure in the blood-vessels of the gland. Now it is found, not only that the gland can be made to secrete in a recently decapitated animal, in which of course there is no blood-pressure, but that, when the circulation is going on, the pressure of the secretion in the duct can rise far beyond that in the gland arteries. Obviously, then, the secretion is no question of mere filtration, since a liquid cannot filter against a higher pressure. Finally, the proof that the vascular dilatation is quite a subsidiary phenomenon has been completed by showing that we can produce all the increased blood-flow through the gland without getting any secretion—that just as in a muscle nerve we can, by curari, paralyze the motor fibres and leave the vaso-dilators intact, so we can by atropin, the active principle of deadly nightshade, get similar phenomena in the gland. In an atropized animal stimulation of the chorda produces vascular dilatation but not a drop of secretion. Bringing blood to the cells abundantly will not make them drink; we must seek something more in the chorda than the vaso-dilator fibres—some proper secretory fibres; that the atropin acts upon them and not upon the gland-cells is shown, as in the muscle, by the fact that the cells still are capable of activity when stimulated otherwise than through the chorda tympani. For example, by stimulation of the sympathetic fibres going to the gland.

So far, then, we seem to have good evidence of a direct action of nerve-fibres upon the gland-cells. But even that is not the whole matter. It is extremely probable, if not certain, that there are two sets of secretory fibres in the gland-nerves: a set which so acts upon the cells as to make them pass on more abundantly the transudation elements of the

secretion (the water and mineral salts), and another, quite different, which governs the chemical transformations of the cells so as to make them produce mucin from mucigen previously stored in them, in a way comparable to the production of trypsin from trypsinogen in the active pancreas. These latter fibres may be called "trophic," since they directly control the cell metabolism: while the former may be called "transudatory" fibres. Some of the evidence which leads to this conclusionis a little complex, but it is worth while to consider it briefly. In the first place, on stimulation of the chorda of an unexhausted gland (that is, a gland not over-fatigued by previous work) the following points can be noted:—

With increasing strength of the stimulus the quantity of the secretion, that is of the water poured out in a unit of time, increases ; at the same time the mineral salts also increase, but more rapidly, so that their percentage in a rapidly formed secretion is greater than in a more slowly formed, up to a certain limit. The percentage of organic constituents of the secretion also increases up to a limit; but soon ceases to rise, or even falls again, while the water and salts still increase. This of course is readily intelligible; since the water and salts can be derived continually from the blood, while the specific elements, coming from the gland-cells, may be soon exhausted; and so far the experiment gives no evidence of the existence of distinct nerve-fibres for the salts and water, and for the specific elements: all vary together with the strength of the stimulus applied to the nerve. But under slightly different circumstances their quantities do not run parallel. The proportion of specific elements in the secretion is largely dependent on whether the gland has been previously excited or not. Prior stimulation, not carried on of course to exhaustion, largely increases the percentage of organic matters in the secretion produced by a subsequent stimulation; but has no effect whatever on the quantities of water and salts. These are governed entirely by the strength of the second stimulation. Here, then, we find that under similar circumstances the transudatory and specific elements of the secretion do not vary together; and are therefore probably dependent upon different exciting causes. And the facts might lead us to suspect that there are in the chorda, besides the vaso-dilator, two

other sets of fibres: one governing the salts and water, and the other the specific elements of the secretion. So far the evidence is, perhaps, not quite conclusive; but experiments upon the parotid gland of the dog put the matter beyond a doubt.

The submaxillary gland receives fibres from the sympathetic system, as well as the *chorda tympani* from the cerebrospinal. Excitation of the sympathetic fibres causes the gland to secrete, but the saliva poured out is different from that following chorda stimulation, which is in the dog abundant and comparatively poor in organic constituents, and accompanied by vascular dilatation: while the "sympathetic saliva," as it is called, is less abundant, very rich in mucin, and accompanied by constriction of the gland arteries. According to the above view we might suppose that the chorda contains many transudatory and few trophic fibres, and the sympathetic many trophic and few transudatory. It might, however, well be objected that the greater richness in organic bodies of the sympathetic saliva was really due to the small quantity of blood reaching the gland, when that nerve was stimulated. This might alter the nutritive phenomena of the cells and cause them to form mucin in unusual abundance, in which case the trophic influence of the nerve would be only indirect. Experiments on the parotid preclude this explanation. That gland, like the submaxillary, gets nerve-fibres from two sources: a cerebral and a sympathetic. The latter enter the gland along its artery, while the former, originating from the glosso-pharyngeal, run in a roundabout course to the gland. Stimulation of the cerebral fibres causes an abundant secretion, rich in water and salts, but with hardly any organic constituents. At the same time it produces dilatation of the gland arteries. Stimulation of the sympathetic causes contraction of the parotid gland arteries and no secretion at all. Nevertheless it causes great changes in the gland-cells. If it be first stimulated for a while and then the cerebral gland-nerve, the resulting secretion may be ten times as rich in organic bodies as that obtained without previous stimulation of the sympathetic; and a similar phenomenon is observed if the two nerves be stimulated simultaneously. So that the sympathetic nerve, though unable of itself to cause a secretion, brings about great chemical changes in the gland-cells. It is a distinct

trophic nerve. This conclusion is confirmed by histology. Sections of the gland after prolonged stimulation of the sympathetic show its cells to be quite altered in appearance, and in their tendency to combine with carmine, when compared either with those of the resting gland or of the gland which has been made to secrete by stimulating its glosso-pharyngeal branch alone.

We have still to meet the objection that the sympathetic fibres may be only indirectly trophic, governing the metabolism of the cells through contraction of the blood-vessels. If this were so, cutting off or diminishing the blood-supply of the gland in any way ought to have the same result as stimulation of its sympathetic fibres. Experiment shows that such is not the case and reduces us to a direct trophic influence of the nerve. When the arteries are closed and the cerebral gland-nerve stimulated, it is found that the percentage of organic constituents in the secretion is as low as usual; it remains almost exactly the same whether the arteries are open or closed or have been previously open or closed. We must conclude that the peculiar influence of the sympathetic does not depend upon its vaso-constrictor fibres.

These observations make it clear that the phenomena of secretion are dependent on very complex conditions, at least in the salivary glands and presumably in others. Primarily dependent upon filtration and dialysis from the blood-vessels and upon the physiological character of the gland-cells, both of these factors are, we find, controlled by the nervous system, such secreting cells being no more automatic than striped muscle; and the facts also give us important evidence of the power of the nervous system to influence cell nutrition directly. In other simpler cases, secretion seems to be a mere direct result of the growth and life of the secreting cell; for example the formation, storage and discharge of fatty matters by the oil-glands of the skin.

Summary. By secretion proper is meant the separation of such substances from the blood as are poured out on free surfaces of the Body, whether external or internal. In its simplest form it is merely a physical process dependent on filtration and dialysis; for example, the elimination of carbon dioxide from the surfaces of the lungs, and very watery liquid poured out on the surface of the serous membranes. Such secretions are known as *transudata,* and their amount is only

indirectly controlled by the nervous system, through the influence of the latter upon the circulation of the blood; they are however dependent on the structure of the cells concerned, so that the characters of the transudata and their quantity are altered when the cells are diseased. After death, too, the process of dialysis through such cells is different from that during life, for the living cell controls to a certain extent the nature and amount of the substances which it will allow to pass through it. The cells lining such surfaces are not, however, secretory tissues in any true sense of the word. In other cases the lining cells are thicker, and more actively concerned in the process; they are then usually spread over the recesses of a much folded membrane, so that the whole is rolled up into a compact organ called a *gland*, the secretion of which may contain only *transudation elements* (as for example that of the lachrymal glands which form the tears) or may contain a *specific element*, formed in the gland by its cells, in addition to transudation elements. In both cases the activity of the organ may be influenced by the nervous system, usually in a reflex manner (*e.g.* the watering of the eyes when the eyeball is touched and the saliva poured into the mouth when food is tasted), but may also be otherwise excited, as for example the flow of tears under the influence of those changes of the central nervous system which are associated with sad emotions, or the watering of the mouth at the thought of dainty food. The nerves going to such glands, besides controlling their blood-vessels, act upon the gland-cells; one set governing the amount of transudation of water and salines which shall take place through them, and another (in the case of glands producing secretions with one or more specific elements) controlling the production of these, by starting new chemical processes in the cells by which a substance built up in them during rest is converted into the specific element, which is soluble in and carried off by the transudation elements. What the specific element of a gland shall be, or whether its secretion contain any, is dependent on the nature of its special cells; how much transudation and how much specific element shall be secreted at any time is controlled by the nervous system; just as the contractility of a muscle depends on the endowments of muscular tissue, and whether it shall rest or contract—and if the latter, how powerfully—upon its nerve.

CHAPTER XX.

The Material Losses of the Body. All day long while life lasts each of us is losing something from his Body. The air breathed into the lungs becomes in them laden with carbon dioxide and water vapor, which are carried off with it when it is expired. The skin is as constantly giving off moisture, the total quantity in twenty-four hours being considerable, even when the amount passed out at any one time is so small as to be evaporated at once and so does not collect as drops of visible perspiration. The kidneys again are constantly at work separating water and certain crystalline nitrogeneous bodies from the blood, along with some mineral salts. The product of kidney activity, however, not being forthwith carried to the surface but to a reservoir, in which it accumulates and which is only emptied at intervals, the activity of those organs appears at first sight intermittent. If to these losses we add certain other waste substances passed into the alimentary canal and got rid of along with the undigested residue of the food, and the loss of hairs and of dried cells from the surface of the skin, it is clear that the total amount of matter daily removed from the Body is considerable. The actual quantity varies with the individual, with the work done, and with the nature of the food eaten; but the following table (p. 300) gives approximately that of the more important daily material losses of an average man.

The living Body thus loses daily in round numbers 4 kilograms of matter (9 lbs.) and, since it is unable to create new matter, this loss must be compensated for from the exterior or the tissues would soon dwindle away altogether; or at least until they were so impaired that life came to an end. After death the losses would be of a different kind, and their quantity much more dependent upon surrounding conditions; but except under very unusual circumstances the wasting away would still continue in the dead Body. Moreover, the compo-

TABLE SHOWING APPROXIMATELY THE AVERAGE DAILY LOSSES OF THE BODY THROUGH LUNGS, KIDNEYS, SKIN, AND ALIMENTARY CANAL.

	Grams.	Grains.		Oxygen.		Carbon.		Hydrogen.		Nitrogen.	
				Grams.	Grains.	Grams.	Grains.	Grams.	Grains.	Grams.	Grains.
Carbon dioxide (CO_2)..	916.5	14114.0	containing	666.5	10284.0	250.0	3850.0				
Water (H_2O).........	3114.5	47963.0	"	2768.5	42685.0	....	....	346.0	5328.0		
Urea (CN_2H_4O)......	34.5	531.0	"	9.0	138.5	7.0	107.5	2.5	38.5	16.0	246.5
Salts—such as sodium chloride, etc.......	32.0	492.8									
Other substances.....	40.0	616.0	"	16.0	246.5	17.0	262.0	4.0	61.5	8.0	46.0
Total.........	4187.5	68716.8		3460.0	53284.0	274.0	4219.5	352.5	5428.0	19.0	292.5

sition of the daily wastes of the living Body is tolerably constant; it does not simply lose a quantity of matter weighing so much, but a certain amount of definite kinds of matter, carbon, nitrogen, oxygen, and so on; and these same substances must be restored to it from outside, in order that life may be continued. To give a stone to one asking for bread might enable him, if he swallowed it, to make up the weight of matter lost in twenty-four hours; but bread would be needed to keep him alive. The Body not only requires a supply of matter from outside, but a supply of certain definite kinds of matter.

The Losses of the Body in Energy. The daily expenditure of matter by the living Body is not the only one: as continuously it loses in some form or another *energy*, or the power of doing work; often as mechanical work expended in moving external objects, but even when at rest energy is constantly being lost to the Body in the form of heat, by radiation and conduction to surrounding objects, by the evaporation of water from the lungs and skin, and by removal in warm excretions. Unless the Body can make energy it must therefore receive a certain supply of it also from the exterior, or it would very soon cease to carry on any of its vital work; it would be unable to move and would cool down to the temperature of surrounding objects. The discoveries of this century having shown that energy is as indestructible and uncreatable (see Physics) as matter, we are led to look for the sources of the supply of it to the Body; and finding that the living Body daily receives it and dies when the supply is cut off, we no longer suppose, with the older physiologists, that it works by means of a mysterious vital force existing in or created by it; but that getting energy from the outside it utilizes it for its purposes—for the performance of its nutritive and other living work—and then returns it to the exterior in what the physicists know as a degraded state; that is, in a less utilizable condition. While energy like matter is indestructible it is, unlike matter, transmutable; iron is always iron and gold always gold; neither can by any means which we possess be converted into any other form of matter; and so the Body, needing carbon, hydrogen, oxygen, and nitrogen to build it and to cover its daily losses, must be supplied with those very substances. As regards energy this is not the case. While the total amount of it in the universe is constant, its form is

constantly subject to change—and that one in which it enters the Body need not be that in which it exists while in it, nor that in which it leaves it. Daily losing heat and mechanical work the Body does not need, could not in fact much utilize energy, supplied to it in these forms; but it does need energy of some form and in amount equivalent to that which it loses.

The Conservation of Energy. The forms of energy yet discovered are not nearly so numerous as the kinds of matter. Still we all know several of them; such as light, heat, sound, electricity, and mechanical work; and most people nowadays know that some of these forms are interconvertible, so that directly or indirectly we can turn one into another. In such changes it is found that a definite amount of one kind always disappears to give rise to a certain quantity of the other; or, in other words, that so much of the first form is equivalent to so much of the second. In a steam-engine, heat is produced in the furnace; when the engine is at work all of this energy does not leave it as heat; some goes as mechanical work, and the more work the engine does the greater is the difference between the heat generated in the furnace and that leaving the machine. If, however, we used the work for rubbing two rough surfaces together we could get the heat back again, and if (which of course is impossible in practice) we could avoid all friction in the moving parts of the machine, the quantity thus restored would be exactly equal to the excess of the heat generated in the furnace over that leaving the engine. Having turned some of the heat into mechanical work we could thus turn the work back into heat again, and find it yield exactly the amount which seemed lost. Or we might use the engine to drive an electro-magnetic machine and so turn part of the heat liberated in its furnace first into mechanical work and that into electricity; and if we chose to use the latter with the proper apparatus, we could turn more or less of it into light, and so have a great part of the energy which first became conspicuous as heat in the engine furnace, now manifested in the form of light at some distant point. In fact, starting with a given quantity of one kind of energy, we may by proper contrivances turn all or some of it into one or more other forms; and if we collected all the final forms and retransformed them into the first, we should have exactly the amount of it which had disappeared when the other kinds appeared. This law, that energy can change its

form but that its amount is invariable, that it cannot be created or destroyed but simply transmuted, is known as the *law of the Conservation of Energy* (see Physics), and, like the indestructibility of matter, lies at the basis of all scientific conceptions of the universe, whether concerned with animate or inanimate objects.

Since all forms of energy are interconvertible it is convenient in comparing amounts of different kinds to express them in terms of some one kind, by saying how much of that standard form the given amount of the kind spoken of would give rise to if completely converted into it. Since the most easily measured form of energy is mechanical work this is commonly taken as the standard form, and the quantities of others are expressed by saying how great a distance against the force of gravity at the earth's surface a given weight could be raised by the energy in question, if it were all spent in lifting the weight. The units of mechanical work being the kilogrammeter or the foot-pound, the *mechanical equivalent* of any given kind of energy is the number of kilogrammeters or foot-pounds of work its unit quantity would perform if converted into mechanical work and used to raise a weight. For example the unit quantity of heat is that necessary to raise one kilogram of water one degree centigrade in temperature; or sometimes, in books written in English, the quantity necessary to warm one pound of water one degree Fahrenheit. When therefore we say that the mechanical equivalent of heat is 423 kilogrammeters we mean that the quantity of heat which would raise one kilogram of water in temperature from 4° C. to 5° C. would, if all turned into mechanical work, be able to raise one kilogram 423 meters against the attraction of the earth; and conversely, that this amount of mechanical work if turned into heat would warm a kilogram of water one degree centigrade. The mechanical equivalent of heat, taking the Fahrenheit thermometric scale and using feet and pounds as measures, is 772 foot-pounds.

Potential and Kinetic Energy. At times energy seems to be lost. Ordinarily we only observe it when it is doing work and producing some change in matter: but sometimes it is at rest, stored away and producing no changes that we recognize and thus seems to have been destroyed. Energy at work is known as *kinetic energy;* energy at rest, not producing changes in matter, is called *potential energy.* Suppose a

stone pulled up by a string and left suspended in the air. We know a certain amount of energy was used to lift it; but while it hangs we have neither heat nor light nor mechanical work to represent it. Still the energy is not lost; we know we have only to cut the string and the weight will fall, and striking something give rise to heat. Or we may wind up a spring and keep it so by a catch. In winding it up a certain amount of energy in the form of mechanical work was used to alter the form of the spring. Until the catch is removed this energy remains stored away as potential energy: but we know it is not lost. Once the spring is let loose again it may drive a clock or a watch, and in so doing will perform again just so much work as was spent in coiling it; and when the watch has run down this energy will all have been turned into other forms—mainly heat developed in the friction of the parts of the watch against one another: but partly also in producing movements of the air, a portion of which we can readily observe in the sound of its ticking. The law of the conservation of energy does not say, then, that either the total potential or the total kinetic energy in the universe is constant in amount: but that the sum of the two is invariable, while constantly undergoing changes from kinetic to potential and *vice versa :* and from one form of kinetic to another.

The Energy of Chemical Affinity. Between every two chemical atoms which are capable of entering into combination there exists a certain amount of potential energy; when they unite this energy is liberated, usually in the form of heat, and once they have combined a certain amount of kinetic energy must be spent to pull them apart again; this being exactly the amount which was liberated when they united. The more stable the compound formed the more kinetic energy appears during its formation, and the more must be spent to break it up again. One may imagine the separated atoms as two balls pushed together by springs, the strength of the spring being proportionate to the degree of their .chemical affinity. Once they are let loose and permitted to strike together the potential energy previously represented by the compressed springs disappears, and in its place we have the kinetic energy, represented by the heat developed when the balls strike together. To pull them apart again, against the springs, to their original positions, just so much mechanical work must be spent as is the equivalent of that amount

of heat which appeared when they struck; and thus kinetic energy will again become latent in breaking up the compound represented by the two in contact. The energy liberated in chemical combination is the most important source of that used in our machines: and also of that spent by the living Body.

The Relation between the Matters Removed from the Body daily and the Energy Spent by it. A working locomotive is, we know, constantly losing matter to the exterior in the form of ashes and gaseous products of combustion, the latter being mainly carbon dioxide and water vapor. The engine also expends energy, not only in the form of heat radiated to the air, but as mechanical work in drawing the cars against the resistance offered by friction or sometimes, up an incline, by gravity. Now the engine-driver knows that there is a close relationship between the losses of matter and the expenditure of energy, so that he has to stoke his furnace more frequently and allow a greater draft of air through it in going up a gradient than when running on the level. The more work the engine does the more coals and air it needs to make up for its greater waste. If we seek the cause of this relationship between work and waste, the first answer naturally is that the engine is a machine the special object of which is to convert heat into mechanical work, and so the more work it has to do the more heat is required for conversion, and consequently the more coals must be burnt. This, however, opens the question of the source of the heat—of all that vast amount of kinetic energy which is liberated in the furnace; and to answer this we must consider in what forms matter and energy enter the furnace, since the energy liberated there must be carried in somehow from outside. For present purposes coals may be considered as consisting of carbon and hydrogen, both of which substances tend to forcibly combine with oxygen at high temperatures, forming in the one case carbon dioxide and in the other water. The oxygen necessary to form these compounds being supplied by the air entering the furnace, all the potential energy of chemical affinity which existed between the uncombined elements becomes kinetic, and is liberated as heat when the combination takes place. The energy utilized by the engine is therefore supplied to it in the form of potential energy, associated with the uncombined forms of matter which reach

the furnace. Once the carbon and hydrogen have combined with oxygen they are no longer of any use as liberators of energy; and the compounds formed if retained in the furnace would only clog it and impede farther combustion; they are therefore got rid of as wastes through the smoke-stack. The engine, in short, receives uncombined elements associated with potential energy; and loses combined elements (which have lost the energy previously associated with them) and kinetic energy: it, so to speak, separates the energy from the matter with which it was connected, utilizes it, and gets rid of the exhausted matter. The amount of kinetic energy liberated during such chemical combinations is very great; a kilogram of carbon uniting with oxygen to form carbon dioxide sets free 8080 units of heat, or calories. During the combination of oxygen and hydrogen to form water even more energy is liberated, one kilogram of hydrogen when completely burnt liberating more than thirty-four thousand of the same units. The mechanical equivalent of this can be calculated if it is remembered that one heat unit = 423 kilogrammeters.

Turning now to the living Body we find that its income and expenditure agree very closely with those of the steam-engine. It receives from the exterior substances capable of entering into chemical union; these combine in it and liberate energy; and it loses kinetic energy and the products of combination. From the outside it takes oxygen through the lungs, and oxidizable substances (in the form of foods) through the alimentary canal; these combine under the conditions prevailing in the living cells just as the carbon and oxygen, which will not unite at ordinary temperatures, combine under the conditions existing in the furnace of the engine; the energy liberated is employed in the work of the Body, while the useless products of combination are got rid of. To explain, then, the fact that our Bodies go on working we have no need to invoke some special mysterious power resident in them and capable of creating energy, a *vital force* having no relation with other natural forces, such as the older physiologists used to imagine. The Body needs and gets a supply of energy from the exterior just as the steam-engine does, food and air being to one what coals and air are to the other; each is a machine in which energy is liberated by chemical combinations and then used for special work;

the character of which depends upon the peculiarities of mechanism which utilizes it in each case, and not upon any peculiarity in the energy utilized or in its source. The Body is, however, a far more economical machine than any steam-engine; of all the energy liberated in the latter only a small fraction, about one eighth, is usefully employed, while our Bodies can utilize for the performance of muscular work alone one fifth of the whole energy supplied to them; leaving out of account altogether the nutritive and other work carried on in them, and the heat lost from them.

The Conditions of Oxidation in the Living Body. Although the general principles applied in the Body and the steam-engine for getting utilizable energy are the same, in minor points obvious differences are found between the two. In the first place the coals of an engine are oxidized only at a very high temperature, one which would be instantly fatal to our Bodies, which, although warm when compared with the bulk of inanimate objects, are very slow fires when compared with a furnace. Chemistry and physics, however, teach us that this difference is quite unimportant so far as concerns the amount of energy liberated. If magnesium wire be ignited in the air it will become white-hot, flame, and leave at the end of a few seconds only a certain amount of incombustible *rust* or *magnesia,* which consists of the metal combined with oxygen. The heat and light evolved in the process represent of course the energy which, in a potential form, was associated with the magnesium and oxygen before their combination. We can, however, oxidize the metal in a different way, attended with no evolution of light and no very perceptible rise of temperature. If, for instance, we leave it in wet air it will become gradually turned into magnesia without having ever been hot to the touch or luminous to the eye. The process will, however, take days or weeks; and while in this slow oxidation just as much energy is liberated as in the former case, it now all takes the form of heat; and instead of being liberated in a short time is spread over a much longer one, as the gradual chemical combination takes place. The slowly oxidizing magnesium is, therefore, at no moment noticeably hot, since it loses its heat to surrounding objects as fast as it is generated. The oxidations occurring in our Bodies are of this slow kind. An ounce of arrowroot oxidized in a fire, and in the Human Body, would

liberate exactly as much energy in one case as the other, but the oxidation would take place in a few minutes and at a high temperature in the former, and slowly, at a lower temperature, in the latter. In the second place, the engine differs from the living Body in the fact that the oxidations in it all take place in a small area, the furnace, and so the temperature there becomes very high; while in our Bodies the oxidations take place all over, in each of the living cells; there is no one furnace or hearth where all the energy is liberated for the whole and transferred thence in one form or another to distant parts: and this is another reason why no one part of the Body attains a very high temperature.

The Fuel of the Body. This is clearly different from that of an ordinary engine: no one could live by eating coals. This difference, again, is subsidiary; a gas-engine requires different fuel from an ordinary locomotive; and the Body requires a somewhat different one from either. It needs, as foods, substances which can, in the first place, be absorbed from the alimentary canal and carried to the various tissues; and, in the second, can be oxidized at a low temperature in the blood or tissues, or can be converted by the living cells into compounds which can be so oxidized. With some trivial exceptions, all substances which fulfil these conditions are complex chemical compounds, and to understand their utilization in the Body we must extend a little the statements above made as to the liberation of energy in chemical combinations. The general law may be stated thus: *Energy is liberated whenever chemical union takes place: and whenever more stable compounds are formed from less stable ones, in which the constituent atoms were less firmly held together.* Of the liberation by simple combination we have already seen an instance in the oxidation of carbon in a furnace; but the union need not be an oxidation. Every one knows how hot quicklime becomes when it is slaked; the water combining strongly with the lime, and energy being liberated in the form of heat during the process. Of the liberation of energy by the breaking down of a complex compound, in which the atoms are only feebly united, into simpler and stabler ones, we get an example in alcoholic fermentation. During that process grape-sugar is broken down into more stable compounds, mainly carbon dioxide and alcohol, while oxygen is at the same time taken up. To pull apart the carbon, hydro-

gen, and oxygen of the sugar molecule requires a certain expenditure of kinetic energy: but in the simultaneous formation of the new and stabler compounds a greater amount of energy is set free, and the difference appears as heat, so that the brewer frequently has to cool his vats with ice. It is by processes like this latter, rather than by direct combinations, that most of the kinetic energy of the Body is obtained; the complex proteids and fats and starches and sugar taken as food being broken down (usually with concomitant oxidation) into simpler and more stable compounds.

Oxidation by Successive Steps. In the furnace of an engine the oxidation takes place completely at once. The carbon and hydrogen leaving it, if it is well managed, are each in the state of their most stable oxygen compound. But this need not be so: we might first oxidize the carbon so as to form carbon monoxide, CO, and get a certain amount of heat; and then oxidize the carbon monoxide farther so as to form carbon dioxide, CO_2, and get more heat. If we add together the amounts of heat liberated in each stage, the sum will be exactly the quantity which would have been obtained if the carbon had been completely burnt to the state of carbon dioxide at first. Every one who has studied chemistry will think of many similar cases. As the process is important physiologically, we may take another example, say the oxidation of alcohol. This may be burnt completely and directly, giving rise to carbon dioxide and water—

$$C_2H_6O + O_6 = 2CO_2 + 3H_2O$$

1 Alcohol.   6 Oxygen.   2 Carbon dioxide.   3 Water.
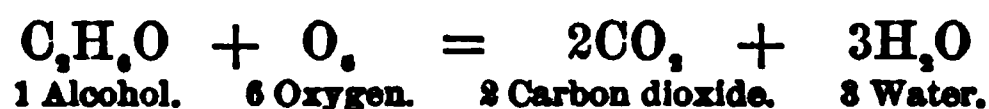
But instead of this we can oxidize the alcohol by stages, getting at each stage only a comparatively small amount of heat evolved. By combining it first with one atom of oxygen, we get aldehyde and water—

$$C_2H_6O + O = C_2H_4O + H_2O$$

1 Alcohol.   1 Oxygen.   1 Aldehyde.   1 Water.
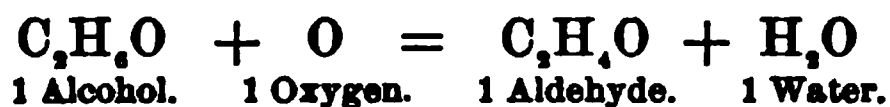
Then we add an atom of oxygen to the aldehyde and get acetic acid (vinegar)—

$$C_2H_4O + O = C_2H_4O_2$$

1 Aldehyde.   1 Oxygen.   1 Acetic acid.

And finally we may oxidize the acetic acid so as to get carbon dioxide and water—

$$C_2H_4O_2 + O_4 = 2CO_2 + 2H_2O.$$
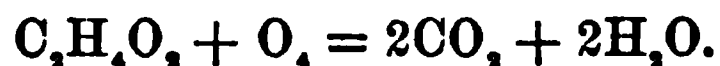
We get, in both cases, from one molecule of alcohol, two of carbon dioxide and three of water; and six atoms of oxygen are taken up. In each stage of the gradual oxidation a certain amount of heat is evolved; and the sum of these is exactly the amount which would have been evolved by burning the alcohol completely at once.

The food taken into the Body is for the most part oxidized in this gradual manner; the products of imperfect combustion in one set of cells being carried off and more completely oxidized in another set, until the final products, no longer capable of further oxidation in the Body, are carried to the lungs, or kidneys, or skin, and got rid of. A great object of physiology is to trace all intermediate compounds between the food which enters and the waste products which leave; to find out just how far chemical degradation is carried in each organ, and what substances are thus formed in various parts: but at present this part of the science is very imperfect.

The Utilization of Energy in the Human Body. In the steam-engine energy is liberated as heat; some of the heat is used to evaporate water and expand the resulting steam; and then the steam to drive a piston. But in the living Body it is very probable (indeed almost certain) that a great part of the energy liberated by chemical transformations does not first take the form of heat; though some of it does. This, again, does not affect the general principle: the source of energy is essentially the same in both cases; it is merely the form which it takes that is different. In a galvanic cell energy is liberated during the union of zinc and sulphuric acid, and we may so arrange matters as to get this energy as heat; but on the other hand we may lead much of it off, as a galvanic current, and use it to drive a magneto-electric machine before it has taken the form of heat at all. In fact, that heat may be used to do mechanical work we must reduce some of it to a lower temperature: an engine needs a condenser of some kind as well as a furnace; and, other things being equal, the cooler the condenser the greater the propor-

tion of the whole heat liberated in the furnace which can be used to do work. Now in a muscle there is no condenser; its temperature is uniform throughout. So when it contracts and lifts a weight, the energy employed must be liberated in some other form than heat—some form which the muscular fibre can use without a condenser.

Summary. The living Body is continually losing matter and expending energy. So long as we regard it as working by virtue of some vital force, the power of generating which it has inherited, the waste is difficult to account for, since it is far more than we can imagine as due merely to wear and tear of the working parts. When, however, we consider the nature of the income of the Body, and of its expenditure, from a chemico-physical point of view, we get the clue to the puzzle. The Body does not waste because it works, but works because it wastes. The working power is obtained by chemical changes occurring in it, associated with the liberation of energy which the living cells utilize; and the products of these chemical changes, being no longer available as sources of energy, are passed out. The chemical changes concerned are mainly the breaking down of complex and unstable chemical compounds into simpler and more stable ones, with concomitant oxidation. Accordingly the material losses of the Body are highly or completely oxidized, tolerably simple, chemical compounds; and its material income is mainly uncombined oxygen and oxidizable substances, the former obtained through the lungs, the latter through the alimentary canal. In energy, its income is the potential energy of uncombined or feebly combined elements, which are capable of combining or of forming more stable compounds; and its final expenditure is kinetic energy almost entirely in the form of mechanical work and heat. Given oxygen, all oxidizable bodies will not serve to keep the Body alive and working, but only those which (1) are capable of absorption from the alimentary canal and (2) those which are oxidizable at the temperature of the Body under the influence of protoplasm. Just as carbon and oxygen will not unite in the furnace of an engine unless the fire be lighted by the application of a match but, when once started, the heat evolved at one point will serve to bring about the conditions of combination through the rest of the mass, so the oxidations of the Body only occur under special conditions; and

these are transmitted from parent to offspring. Every new Human Being starts as a portion of protoplasm separated from a parent and affording the conditions for those chemical combinations which supply to living matter its working power: this serves, like the energy of the burning part of a fire to start similar processes in other portions of matter. At present we know nothing in physiology answering to the match which lights a furnace; those manifestations of energy which we call life are handed down from generation to generation, as the sacred fire in the temple of Vesta from one watcher to another. Science may at some time teach us how to bring the chemical constituents of protoplasm into that combination in which they possess the faculty of starting oxidations under those conditions which characterize life; then we shall have learnt to strike the vital match. For the present we must be content to study the properties of that form of matter which possesses living faculties; since there is no satisfactory proof that it has ever been produced, within our experience, apart from the influence of matter already living. How the vital spark first originated, how molecules of carbon, hydrogen, nitrogen and oxygen first united with water and salts to form protoplasm, we have no scientific data to ground a positive opinion upon, and such as we may have must rest upon other grounds.

CHAPTER XX.

FOODS.

Foods as Tissue-formers. Hitherto we have considered foods merely as source of energy, but they are also required to build up the substance of the Body. From birth to manhood we increase in bulk and weight, and that not merely by accumulating water and such substances, but by forming more bone, more muscle, more brain, and so on, from materials which are not necessarily bone or muscle or nerve-tissue. Alongside of the processes by which complex substances are broken down and oxidized and energy liberated, constructive processes take place by which new complex bodies are formed from simpler substances taken as food. A great part of the energy liberated in the Body is in fact utilized first for this purpose, since to construct complex unstable molecules, like those of protoplasm, from the simpler compounds taken into the Body, needs an expenditure of kinetic energy. Even after full growth, when the Body ceases to gain weight, the same synthetic processes go on; the living tissues are steadily broken down and constantly reconstructed, as we see illustrated by the condition of a man who has been starved for some time, and who loses not only his power of doing work and of maintaining his bodily temperature but also a great part of his living tissues. If again fed properly he soon makes new fat and new muscle and regains his original mass. Another illustration of the continuance of constructive powers during the whole of life is afforded by the growth of the muscles when exercised properly.

Since the tissues, on ultimate analysis, yield mainly carbon, hydrogen, nitrogen and oxygen, it might be supposed *a priori* that a supply of these elements in the uncombined state would serve as material for the constructive forces of the Body to work with. Experience, however, teaches us that this is not the case, but that the animal body requires, for the most part, highly complex compounds for the con-

struction of new tissue elements. All the active tissues yield on analysis large quantities of proteids which, as pointed out in Chapter I, enter always into the structure of protoplasm. Now, so far as we know at present,* the animal body is unable to build up proteids from simpler compounds of nitrogen, although when given one variety of them it can convert that one into others, and combine them with other things to form protoplasm. Hence proteids are an essential article of diet, in order to replace the proteid of the living cells which is daily broken down and eliminated in the form of urea and other waste substances. Even albuminoids (p. 10), although so nearly allied to proteids, will not serve to replace them entirely in a diet; a man fed abundantly on gelatine, fats, and starches would starve as certainly, though not so quickly, as if he got no nitrogenous food at all: his tissue waste would not be made good, and he would at last be no more able to utilize the energy-yielding materials supplied to him than a worn-out steam-engine could employ the heat of a fire in its furnace. So, too, the animal is unable to take the carbon for the construction of its tissues, from such simple compounds as carbon dioxide.* Its constructive power is limited to the utilization of the carbon contained in more complex and less stable compounds, such as proteids, fats or sugars.

Nearly all the tissue-forming foods must therefore consist of complex substances, and of these a part must be proteids, since the Body can utilize nitrogen for tissue formation only when supplied with it in that form. The bodies thus taken in are sooner or later broken down into simpler ones and eliminated; some at once in order to yield energy, others only after having first been built up into part of a living cell. The partial exceptions afforded by such losses to the Body as milk for suckling the young, or the albuminous and fatty bodies stored for the same purpose in the egg of a bird, are only apparent; the chemical degradation is only postponed, taking place in the body of the offspring instead of that of the parent. In all cases animals are thus, essentially, proteid consumers or wasters, and breakers down of complex bodies; the carbon, hydrogen, and nitrogen which they take as foods in the form of complex unstable bodies, ultimately leaving

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* There is some reason to believe that some few of the lower animals which contain chlorophyl can manufacture proteids and utilize carbon dioxide.

them in the simpler compounds, carbon dioxide, water, and urea; which are incapable of either yielding energy or building tissue for any other animal and so of serving it as food. The question immediately suggests itself—How, since animals are constantly breaking up these complex bodies and cannot again build them, is the supply kept up ? For example, the supply of proteids, substances which cannot be made artificially by any process which we know, and yet are necessary foods for all animals, and daily destroyed by them.

The Food of Plants. As regards our own Bodies the question at the end of the last paragraph might perhaps be answered by saying that we get our proteids from the flesh of the other animals which we eat. But, then, we have to account for the possession of them by those animals; since they cannot make them from urea and carbon dioxide and water any more than we can. The animals eaten get them, in fact, from plants which are the great proteid formers of the world, so that the most carnivorous animal really depends for its most essential foods upon the vegetable kingdom; the fox that devours a hare in the long-run lives on the proteids of the herbs that the hare had previously eaten. All animals are thus, in a certain sense, parasites; they only do half of their own nutritive work, just the final stages, leaving all the rest to the vegetable kingdom and using the products of its labor ; and plants are able to meet this demand because they can live on the simple compounds of carbon, hydrogen, and nitrogen eliminated by animals, building up out of them new complex substances which animals can use as food. A green plant, supplied with ammonium salts, carbon dioxide, water, and some minerals, will grow and build up large quantities of proteids, fats, starches, and similar things; it will pull the stable compounds eliminated by animals to pieces, and build them up into complex unstable bodies, capable of yielding energy when again broken down. However, to do such work, to break up stable combinations and make from them less stable, needs a supply of kinetic energy which disappears in the process, being stored away as potential energy in the new compound; and we may ask whence it is that the plant gets the supply of energy which it thus utilizes for chemical construction, since its simple and highly oxidized foods can yield it none. It has been proved that for this purpose the green plant uses the energy of sunlight: those of its cells which con-

tain the substance called *chlorophyl* (leaf green) have the power of utilizing energy in the form of light for the performance of chemical work, just as a steam-engine can utilize heat for the performance of mechanical work. Exposed to light, and receiving carbon dioxide from the air, and water and ammonia (which is produced by the decomposition of urea) and other simple nitrogen compounds from the soil, the plant builds them up again, with the elimination of oxygen, into complex bodies like those which animals broke down with fixation of oxygen. Some of the bodies thus formed it uses for its own growth and the formation of new protoplasm, just as an animal does; but in sunlight it forms more than it uses, and the excess stored up in its tissues is used by animals. In the long-run, then, all the energy spent by our Bodies comes through millions of miles of space from the sun; but to seek the source of its supply there would take us far out of the domain of Physiology.

Non-oxidizable Foods. Besides our oxidizable foods, a large number of necessary food-materials are not oxidizable, or at least are not oxidized in the Body. Typical instances are afforded by water and common salt. The use of these is in great part physical: the water, for instance, dissolves materials in the alimentary canal, and carries the solutions through the walls of the digestive tube into the blood and lymph vessels, so that they can be carried from part to part; and it permits interchanges to go on by diffusion. The salines also influence the solubility and chemical interchanges of other things present with them. Serum albumen, the chief proteid of the blood, for example, is insoluble in pure water, but dissolves readily if a small quantity of neutral salts is present. Besides such uses the non-oxidizable foods have probably others, in what we may call machinery formation. In the salts which give their hardness to the bones and teeth, we have an example of such an employment of them: and to a less extent the same may be true of other tissues. The Body, in fact, is not a mere store of potential energy, but something more—it is a machine for the disposal of it in certain ways; and, wherever practicable, it is clearly advantageous to have the purely energy-expending parts made of non-oxidizable matters, and so protected from change and the necessity of frequent renewal. The Body is a self-building and self-repairing machine, and the material for this

building and repair must be supplied in the food, as well as the fuels, or oxidizable foods, which yield the energy the machine expends; and while experience shows us that even for machinery construction oxidizable matters are largely needed, it is nevertheless a gain to replace them by non-oxidizable substances when possible; just as if practicable it would be advantageous to construct an engine out of materials which would not rust, although other conditions determine the use of iron for the greater part of it.

Definition of Foods. *Foods may be defined as substances which, when taken into the alimentary canal, are absorbed from it, and then serve either to supply material for the growth of the Body, or for the replacement of matter which has been removed from it, either after oxidation or without having been oxidized.* Foods to replace matters which have been oxidized must be themselves oxidizable; they are *force-generators*, but may be and generally are also tissue-formers; and are nearly always complex organic substances derived from other animals or from plants. Foods to replace matters not oxidized in the Body are *force-regulators*, and are for the most part tolerably simple inorganic compounds. Among the force-regulators we must, however, include certain organic foods which, although oxidized in the Body and serving as liberators of energy, yet produce effects totally disproportionate to the energy they set free, and for which effects they are taken. In other words, their influence as stimuli in exciting certain tissues to liberate energy, or as inhibitory agents checking the activity of parts, is more marked than their direct action as force-generators. As examples, we may take condiments: mustard and pepper are not of much use as sources of energy, although they no doubt yield some; we take them for their stimulating effect on the mouth and other parts of the alimentary canal, by which they promote an increased flow of the digestive secretions or an increased appetite for food. Thein and caffein, the active principles of tea and coffee, are taken for their stimulating effect on the nervous system, rather than for the amount of energy yielded by their own oxidation.

Conditions which a Food must Fulfil. (1) A food must contain the elements which it is to replace in the Body: but that alone is not sufficient. The elements leaving the Body being usually derived from the breaking down of com-

plex substances in it, the food must contain them either in the form of such complex substances, or in forms which the Body can build up into them, Free nitrogen and hydrogen are no use as foods, since they are neither oxidizable under the conditions prevailing in the Body (and consequently cannot yield it energy), nor are they capable of construction by it into its tissues. (2) Food after it has been swallowed is still in a strict sense outside the Body; the alimentary canal is merely a tube running through it, and so long as food lies there it does not form any part of the Body proper. Hence foods must be capable of absorption from the alimentary canal; either directly, or after they have been changed by the processes of digestion. Carbon, for example, is useless as food, not merely because the Body could not build it up into its own tissues, but because it cannot be absorbed from the alimentary canal. (3) Neither the substance itself nor any of the products of its transformation in the Body must be injurious to the structure or activity of any organ. If so it is a *poison*, not a food.

Alimentary Principles. The articles which in common language we call foods are, in most cases, mixtures of several *foodstuffs*, with substances which are not foods at all. Bread, for example, contains water, salts, gluten (a proteid), some fats, much starch, and a little sugar; all true foodstuffs: but mixed with these is a quantity of *cellulose* (the chief chemical constituent of the walls which surround vegetable cells), and this is not a food since it is incapable of absorption from the alimentary canal. Chemical examination of all the common articles of diet shows that the actual number of important foodstuffs is but small: they are repeated in various proportions in the different things we eat, mixed with small quantities of different flavoring substances, and so give us a pleasing variety in our meals; but the essential substances are much the same in the fare of the workman and in the "delicacies of the season." These primary foodstuffs, which are found repeated in so many different foods, are known as "*alimentary principles*"; and the physiological value of any article of diet depends on them far more than on the traces of flavoring matters which cause certain things to be especially sought after and so raise their market value. The alimentary principles may be conveniently classified into

proteids, albuminoids, hydrocarbons, carbohydrates, and inorganic bodies.

Proteid or Albuminous Alimentary Principles. Of the nitrogenous foodstuffs the most important are proteids: they form an essential part of all diets, and are obtained both from animals and plants. The most common and abundant are myosin and syntonin, which exist in the lean of all meats; egg albumen; casein, found in milk and cheese; gluten and vegetable casein from various plants.

Gelatinoid or Albuminoid Alimentary Principles. These also contain nitrogen, but cannot replace the proteids entirely as foods; though a man can get on with less proteids when he has some albuminoids in addition. The most important is *gelatin*, which is yielded by the white fibrous tissue of animals when cooked. On the whole the gelatinoids are not foods of high value, and the calf's-foot jelly and such compounds, often given to invalids, have not nearly the nutritive value they are commonly supposed to possess.

Hydrocarbons (*Fats and Oils*). The most important are stearin, palmatin, and olein, which exist in various proportions in animal fats and vegetable oils; the more fluid containing more olein. Butter contains also a little of a fat named butyrin. Fats are compounds of glycerine and fatty acids, and any such substance which is fusible at the temperature of the Body will serve as a food. The stearin of beef and mutton fats is not by itself fusible at the body temperature, but is mixed in those foods with so much olein as to be melted in the alimentary canal. Beeswax, on the other hand, is a fatty body which will not melt in the intestines and so passes on unabsorbed; although from its composition it would be useful as a food could it be digested. A distinction is sometimes made between *fats* proper (the adipose tissue of animals consisting of fatty compounds inclosed in albuminous cell-walls) and *oils*, or fatty bodies which are not so organized.

Carbohydrates. These are mainly of vegetable origin. The most important are *starch*, found in nearly all vegetable foods ; *dextrin* ; *gums* ; *grape-sugar*, called also *dextrose* or *glucose* (into which starch is converted during digestion); and *cane-sugar*. *Sugar of milk* and *glycogen* are alimentary principles of this group, derived from animals. All of them, like the fats, consist of carbon, hydrogen and oxygen; but the per-

centage of oxygen in them is much higher, there being one atom of oxygen for every two of hydrogen in their molecule.

Inorganic Foods. Water; common salt; and the chlorides, phosphates, and sulphates of potassium, magnesium and calcium. More or less of these bodies, or the materials for their formation, exists in all ordinary articles of diet, so that we do not swallow them in a separate form. Phosphates, for example, exist in nearly all animal and vegetable foods; while other foods, as casein, contain phosphorus in combinations which in the Body yield it up to be oxidized to form phosphoric acid. The same is true of sulphates, which are partially swallowed as such in various articles of diet, and are partly formed in the Body by the oxidation of the sulphur of various proteids. Calcium salts are abundant in bread, and are also found in many drinking-waters. Water and table-salt form exceptions to the rule that inorganic bodies are eaten imperceptibly along with other things, since the Body loses more of each daily than is usually supplied in that way. It has, however, been maintained that salt, as such, is an unnecessary luxury; and there seems some evidence that certain savage tribes live without more than they get in the meat and vegetables they eat. Such tribes are, however, said to suffer especially from intestinal parasites; and there is no doubt that to civilized man the absence of salt is a great privation.

Calcium seems to be an essential constituent of all living cells and in some way closely connected with the manifestation of their activity. As previously mentioned the heart of a frog after thorough irrigation with dilute solution of sodium chloride ceases to beat, but resumes its pulsations when a minute trace of calcium chloride is added to the solution; and while ordinary serum restores the beat of such a washed-out heart, serum from which all its calcium has been removed does not. Moreover if defibrinated blood to which a little more sodium oxalate than is sufficient to precipitate all its calcium has been added, be circulated through the vessels of a muscle, the latter loses its contractility, apparently because the slight excess of oxalate precipitates the calcium of the muscle-fibres; for the contractility may be restored by supplying some dissolved calcium chloride. Nerves treated similarly lose their irritability; and the eggs of some aquatic

animals will not develop normally in water from which all calcium salts have been removed.

Mixed Foods. These, as already pointed out, include nearly all common articles of diet; they contain more than one alimentary principle. Among them we find great differences; some being rich in proteids, others in starch, others in fats, and so on. The formation of a scientific dietary depends on a knowledge of these characteristics. The foods eaten by man are, however, so varied that we cannot do more than consider the most important.

Flesh. This, whether derived from bird, beast, or fish, consists essentially of the same things—muscular fibres, connective tissue and tendons, fats, blood-vessels, and nerves. It contains several proteids, especially myosin; gelatin-yielding matters in the white fibrous tissue; stearin, palmatin, and olein as representatives of the fats; and a small amount of carbohydrates in the form of glycogen and grape-sugar, or some chemically allied substances. Flesh also contains much water and a considerable number of salines, the most important and abundant being potassium phosphate. *Osmazome* is a crystalline nitrogenous body which gives much of its taste to flesh; and small quantities of various similar substances exist in different kinds of meat. There is also more or less yellow elastic tissue in flesh; it is indigestible and useless as food.

When meat is cooked its white fibrous tissue is turned into gelatin, and the whole mass becomes thus softer and more easily disintegrated by the teeth. When boiled some of the proteid matters of the meat pass out into the broth, and there in part coagulate and form the *scum:* this loss may be prevented in great part by putting the raw meat at once into boiling water which coagulates the surface albumen before it dissolves out, and this keeps in the rest, while the subsequent cooking is continued slowly. In any case the myosin, being insoluble in water, remains behind in the boiled meat. In baking or roasting, all the solid parts of the flesh are preserved and certain agreeably flavored bodies are produced, as to the nature of which little is known.

Eggs. These contain a large amount of egg albumen and, in the yolk, another proteid, known as vitellin. Also fats, and a substance known as *lecithin*, which is important as containing a considerable quantity of phosphorus. Leci-

thin, or rather a substance yielding it, is an important con-
stituent of the nervous tissues.

Milk contains a proteid, *caseinogen;* several fats in the
butter; a carbohydrate, *milk-sugar;* much water; and salts,
especially potassium and calcium phosphates. *Butter* consists
mainly of the same fats as those in beef and mutton; but has
in it about one per cent of a special fat, butyrin. In the milk
it is disseminated in the form of minute globules which, for
the most part, float up to the top when the milk is let stand
and then form the *cream.* In this each fat-droplet is sur-
rounded by a pellicle of albuminous matter; by churning,
these pellicles are broken up and the fat-droplets then run to-
gether to form the butter. Caseinogen is insoluble in water;
in milk it is dissolved by the alkaline salts present. When
milk is kept, its sugar ferments and gives rise to lactic acid,
which neutralizes the alkali and precipitates the caseinogen
as *curds.* In cheese-making the caseinogen is acted upon by
a ferment (*rennin*) present in the extract of stomach used,
and converted into *tyrein* which is precipitated: this clotting
does not take place unless a calcium salt be present. Tyrein,
which forms the main bulk of a true cheese, is different from
the curd precipitated from milk by acids; cheese made from
the latter does not " ripen." Caseinogen is frequently called
casein, which name should be given to the tyrein formed from
caseinogen by ferment action.

Vegetable Foods. Of these wheat affords the best. In
1000 parts it contains 135 of proteids, 568 of starch, 46 of
dextrin (a carbohydrate), 49 of grape-sugar, 19 of fats, and
32 of cellulose, the remainder being water and salts. The
proteid of wheat is mainly *gluten,* which when moistened
with water forms a tenacious mass, and this it is to which
wheaten bread owes its superiority. When the dough is
made yeast is added to it, and produces a fermentation by
which, among other things, carbon dioxide gas is produced.
This gas, imprisoned in the tenacious dough, and expanded
during baking, forms cavities in it and causes it to "rise"
and make "light bread," which is not only more pleasant to
eat but more digestible than heavy. Other cereals may con-
tain a larger percentage of starch, but none have so much
gluten as wheat; when bread is made from them the carbon
dioxide gas escapes so readily from the less tenacious dough
that it does not expand the mass properly. *Corn* contains in

1000 parts, 79 of proteids, 637 of starch, and from 50 to 87 of fats; much more than any other kind of grain. *Rice* is poor in proteids (56 parts in 1000) but very rich in starch (823 parts in 1000). *Peas* and *beans* are rich in proteids (from 220 to 260 parts in 1000), and contain about half their weight of starch. *Potatoes* are a poor food. They contain a great deal of water and cellulose, and only about 13 parts of proteids and 154 of starch in 1000. Other fresh vegetables, as carrots, turnips, and cabbages, are valuable mainly for the salts they contain; their weight is mainly due to water, and they contain but little starch, proteids, or fats. Fruits, like most fresh vegetables, are mainly valuable for their saline constituents, the other foodstuffs in them being only present in small proportion. Some fruit or vegetable is, however, a necessary article of diet; as shown by the scurvy which used to prevail among sailors before fresh or canned vegetables and lime-juice were supplied to them.

The Cooking of Vegetables. This is of more importance even than the cooking of flesh, since in most the main alimentary principle is starch, and raw starch is difficult of digestion. In plants starch is nearly always stored up in the form of solid granules, which consist of alternating layers of *starch cellulose* and *starch granulose.* The digestive fluids turn the starch into sugars which are soluble and can be absorbed from the alimentary canal, while starch itself cannot. These fluids act slowly and imperfectly on raw starch, and then only on the granulose; but when boiled, the starch granules swell up, and become more readily converted into sugars, and the starch cellulose is so altered that it too undergoes that change. When starch is roasted it is in part turned into a substance known as soluble starch which is readily dissolved in the alimentary canal. There is, therefore, a scientific foundation for the common belief that the crust of a loaf is more digestible than the crumb, and toast than ordinary bread.

Alcohol. There are perhaps no common articles of diet concerning which more contradictory statements have been made than alcoholic drinks. This depends upon their peculiar position: according to circumstances alcohol may be a poison or be useful; when useful it may be regarded either as a force-regulator or a force-generator. It is sometimes a valuable medicine, but it does no good to the healthy body.

If not more than two ounces (which would be contained in about four ounces of whiskey or two quarts of lager-beer) are taken in the twenty-four hours, they are completely oxidized in the Body and excreted as water and carbon dioxide. In this oxidation energy is of course liberated and can be utilized. Commonly, however, alcohol is not taken for this purpose but as a force-regulator, for its influence on the nervous system or digestive organs, and it is in this capacity that it becomes dangerous. For not only may it be taken in quantities so great that it is not at all oxidized in the Body but is passed through it as alcohol, or even that it acts as a narcotic poison instead of a stimulant, but when taken in what is called moderation there can be no doubt that the constant " whipping up " of the flagging organs, if continued, must be dangerous to their integrity. Hence the daily use of alcohol merely in such quantities as to produce slight exhilaration or to facilitate work is by no means safe; though in disease when the system wants rousing to make some special effort, the physician cannot dispense with it or some other similarly acting substance. In fact, as a force-generator alcohol may be advantageously replaced by other foods in nearly all cases; and there is no evidence that it helps in the construction of the working tissues, though its excessive use often leads to an abnormal accumulation of fat. Its proper use is as a " whip," and one has no more right to use it to the healthy Body than the lash to overdrive a willing horse. The physician is the proper person to determine whether it is wanted under any given circumstances.

If alcohol is used as a daily article of diet it should be borne in mind that when concentrated it may chemically alter the proteids of the cells of the stomach with which it comes in contact, in the same sort of way, though of course to a much less degree, as it shrivels and dries up an animal preserved in it. Dilute alcoholic drinks, such as claret and beer, are therefore far less baneful than whiskey or brandy, and these are, so far as direct action on the stomach is concerned, worse the less they are diluted. For the same reason alcoholic drinks are far more injurious on an empty stomach than after a meal. When the stomach is full the liquor is diluted, is more slowly absorbed, and, moreover, is largely used up in coagulating the proteids of the food instead of those of the gastric lining membrane. The old " three

bottle" men who drank their port-wine after a heavy dinner, got off far more safely than the modern tippler who is taking "nips" all day long, although the latter may imbibe a smaller quantity of alcohol in the twenty-four hours. By far the best way, however, is to avoid alcohol altogether in health. If the facts lead us to conclude that under some conditions it may be to a certain extent a food, it is a dangerous one: even in what we may call "physiological" quantities, or such amounts as can be totally oxidized in the Body.

The Advantage of a Mixed Diet. The necessary quantity of daily food depends upon that of the material daily lost from the Body, and this varies both in kind and amount with the energy expended and the organs most used. In children a certain excess beyond this is required to furnish materials for growth. Although it is impossible to lay down with perfect accuracy how much daily food any individual requires, still the average quantity may be derived from the table of daily losses given on page 300, which shows that a healthy man needs daily in assimilable forms about 274 grams (4220 grains) of carbon and 19 grams (292 grains) of nitrogen. The daily loss of hydrogen, which is very great (352 grams or 5428 grains), is for the most part made good by water which has been drunk and, so to speak, merely filtered through the Body, after having assisted in the solution and transference through it of other substances. About 300 grams (4620 grains) of water containing 33.3 grams (513 grains) of hydrogen are, however, formed in the Body by oxidation, and the hydrogen for this purpose must be supplied in the form of some oxidizable foodstuff, whether proteid, fat, or carbohydrate. The oxygen eliminated is mainly received from the air through the lungs, but some is taken in combination in the food.

Since proteid foods contain carbon, nitrogen and hydrogen, life may be kept up on them alone, with the necessary salts, water and oxygen; but such a form of feeding would be anything but economical. Ordinary proteids contain in 100 parts (p. 9) about 52 of carbon and 15 of nitrogen, so a man fed on them alone would get about 3½ parts of carbon for every 1 of nitrogen. His daily losses are not in this ratio, but about that of 274 grams (4220 grains) of carbon to 20 grams (308 grains) of nitrogen, or as 13.7 to 1; and so to get enough carbon from proteids far more than the necessary

amount of nitrogen must be taken. Of dry proteids 527 grams (8116 grains) would yield the necessary carbon, but would contain 79 grams (1217 grains) of nitrogen; or four times more than is required to cover the necessary daily losses of that element. Fed on a purely proteid diet a man would, therefore, have to digest a vast quantity to get enough carbon, and in eating and absorbing it, as well as in getting rid of the extra nitrogen which is useless to him, a great deal of unnecessary labor would be thrown upon the various organs of his Body. Similarly, if a man were to live on bread alone he would burden his organs with much useless work. For bread contains but little nitrogen in proportion to its carbon, and so, to get enough of the former, far more carbonaceous substances than could be utilized would have to be eaten, digested and eliminated daily.

Accordingly, we find that mankind in general employ a mixed diet when they can get it, using richly proteid substances to supply the nitrogen needed, but deriving the carbon mainly from non-nitrogenous foods of the fatty or carbohydrate groups, and so avoiding excess of either. For instance, lean beef contains about ¼ of its weight of dry proteid, which contains 15 per cent of nitrogen. Consequently the 133 grams (2048 grains) of proteid which would be found in 532 grams (1 lb. 3 oz.) of lean meat would supply all the nitrogen needed to compensate for a day's losses. But the proteid contains 52 per cent of carbon, so the amount of it in the above weight of fatless meat would be 69 grams (1062 grains) of carbon, leaving 205 grams (3157 grains) to be got either from fats or carbohydrates. The necessary amount would be contained in about 256 grams (3942 grains) of ordinary fats or 460 grams (7084 grains) of starch; hence either of these, with the above quantity of lean meat, would form a far better diet, both for the purse and the system, than the meat alone.

As already pointed out, nearly all common foods contain several *foodstuffs*. Good butcher's meat, for example, contains nearly half its dry weight of fat; and bread, besides proteids, contains starch, fats and sugar. In none of them, however, are the foodstuffs mixed in the physiologically best proportions, and the practice of employing several of them at each meal, or different ones at different meals, during the day, is thus not only agreeable to the palate but in a high degree advantageous to the Body. The strict vegetarians who do

not employ even such substances as eggs, cheese and milk, but confine themselves to a purely vegetable diet (such as is always poor in proteids), daily take far more carbon than they require, and are to be congratulated on their excellent digestions which are able to stand the strain. Those who use eggs, cheese, etc., can of course get on very well, since such substances are extremely rich in proteids, and supply the nitrogen needed without the necessity of swallowing the vast bulk of food which must be eaten in order to get it from plants directly.

CHAPTER XXII.

THE ALIMENTARY CANAL AND ITS APPENDAGES.

General Arrangement. The alimentary canal is essentially a tube running through the Body (Fig. 2) and lined by a vascular membrane, most of which is specially adapted for absorption; it communicates with the exterior at three points (the nose, the mouth, and the anal aperture), at which the lining *mucous membrane* is continuous with the general outer integument. Supporting the absorbent membrane are layers which strengthen the tube, and are in part muscular and, by their contractions, serve to pass materials along it from one end to the other. In the walls of the canal are numerous blood and lymphatic vessels which carry off the matters absorbed from its cavity; and there also exist in connection with it numerous glands, whose function it is to pour into it various secretions which exert a solvent influence on such foodstuffs as would otherwise escape absorption. Some of these glands are minute and imbedded in the walls of the alimentary tube itself, but others (such as the salivary glands) are larger and lie away from the main channel, into which their products are carried by ducts of various lengths.

The alimentary tube is not uniform but presents several dilatations on its course; nor is it straight, since, being much longer than the Body, a large part of it is packed away by being coiled up in the abdominal cavity.

Subdivisions of the Alimentary Canal. The mouth-opening leads into a chamber containing the teeth and tongue, the *mouth-chamber* or *buccal cavity.* This is succeeded by the *pharynx* or *throat-cavity,* which narrows at the top of the neck into the *gullet* or *œsophagus;* this runs down through the thorax and, passing through the diaphragm, dilates in the upper part of the abdominal cavity into the *stomach.* Beyond the stomach the channel again narrows to form a long and greatly coiled tube, the *small intestine,* which terminates by opening into the *large intes-*

tine, much shorter although wider than the small, and terminating by an opening on the exterior.

The Mouth - cavity (Fig. 105) is bounded in front and on the sides by the lips and cheeks, below by the tongue, *k*, and above by the *palate;* which latter consists of an anterior part, *l*, supported by bone and called the *hard palate*, and a posterior, *f*, containing no bone, and called the *soft palate.* The two can readily be distinguished by applying the tip of the tongue to the roof of the mouth and drawing it backwards. The hard palate forms the partition between the mouth and nose. The soft palate arches down over the back of the mouth, hanging like a curtain between it and the pharynx, as can be seen by holding the mouth open in front of a looking-glass. From the middle of its free border a conical process, the *uvula*, hangs down.

Fig. 105.—The mouth, nose and pharynx, with the commencement of the gullet and larynx, as exposed by a section, a little to the left of the median plane of the head. *a*, vertebral column ; *b*, gullet ; *c*, windpipe ; *d*, larynx ; *e*, epiglottis ; *f*, soft palate ; *g*, opening of Eustachian tube ; *k*, tongue ; *l*, hard palate ; *m*, the sphenoid bone on the base of the skull ; *n*, the fore part of the cranial cavity ; *o*, *p*, *q*, the turbinate bones of the outer side of the left nostril-chamber.

The Teeth. Immediately within the cheeks and lips are two semicircles, formed by the borders of the upper and lower jaw-bones, which are covered by the *gums*, except at intervals along their edges where they contain sockets in which the teeth are implanted. During life two sets of teeth are developed; the first or *milk set* appears soon after birth and is shed during childhood, when the second or *permanent set* appears.

The teeth differ in minor points from one another, but in each three parts are distinguishable; one, seen in the mouth and called the *crown* of the tooth; a second, imbedded in the jaw-bone and called the *root* or *fang;* and between the two,

embraced by the edge of the gum, is a narrowed portion, the *neck* or *cervix*. From differences in their forms and uses the teeth are divided into *incisors, canines, bicuspids* and *molars,* arranged in a definite order in each jaw. Beginning at the middle line we meet in each half of each jaw with, successively, two incisors, one canine, and two molars in the milk set; making twenty altogether in the two jaws. The teeth of the permanent set are thirty-two in number, eight in each half of each jaw, viz.—beginning at the middle line— two incisors, one canine, two bicuspids, and three molars. The bicuspids, or premolars, of the permanent set replace the milk molars, while the permanent molars are new teeth added on as the jaw grows, and not substituting any of the milk-teeth. The hindmost permanent molars are often called the *wisdom-teeth.*

Characters of Individual Teeth. The *incisors* (Fig. 106) are adapted for cutting the food. Their crowns are chisel-shaped and have sharp horizontal cutting edges, which become worn away by use so that they are bevelled off behind in the upper row, and in the opposite direction in the lower. Each has a single long fang. The *canines* (Fig. 107) are somewhat larger than the incisors. Their crowns are thick and somewhat conical, having a central point or *cusp* on the cutting edge. In dogs, cats and other *carnivora* the canines are very large and adapted for seizing and holding prey. The *bicuspids* or *premolars* (Fig. 108) are rather shorter than

FIG. 106.   FIG. 10   FIG. 108.   FIG. 109.

FIG. 106.—An incisor tooth.
FIG. 107.—A canine or eye tooth.
FIG. 108.—A bicuspid tooth seen from its outer side; the inner cusp is, accordingly, not visible.
FIG. 109.—A molar tooth.

the canines and their crowns are somewhat cuboidal. Each has two cusps, an outer towards the cheek, and an inner on the side turned towards the interior of the mouth. The fang

is compressed laterally, and has usually a groove partially subdividing it into two. At its tip the separation is often complete. The *molar teeth* or *grinders* (Fig. 109) have large crowns with broad surfaces, on which are four or five projecting tubercles, which roughen them and make them better adapted to crush the food. Each has usually several fangs. The *milk-teeth* only differ in subsidiary points from those of the same names in the permanent set.

The Structure of a Tooth. If a tooth be broken open, a cavity extending through both crown and fang will be found in it. This is filled during life with a soft vascular pulp, and hence is known as the " pulp-cavity " (*c*, Fig. 110). The hard parts of the tooth disposed around the pulp-cavity consist of three different tissues. Of these one immediately surrounds the cavity and makes up most of the bulk of the tooth; it is *dentine* (2, Fig. 110); covering the dentine on the crown is the *enamel* (1, Fig. 110) and, on the fang, the *cement* (3, Fig. 110).

The pulp-cavity opens below by a narrow aperture at the tip of the fang, or at the tip of each if the tooth have more than one. The pulp consists mainly of connective tissue, but its surface next the dentine is covered by a layer of columnar cells. Through the opening on the fang blood-vessels and. nerves enter the pulp.

The dentine (ivory) yields on analysis the same materials as bone but is somewhat harder, earthy matters constituting 72 per cent of it as against CG per cent in bone. Under the microscope it is recognized by the fine *dentinal tubules* which, radiating from the pulp-cavity, perforate it throughout, finally ending in minute branches which open into irregular cavities, the *interglobular spaces*, which lie just beneath the enamel or cement. At their widest ends, close to the pulp-cavity, the dentinal tubules are only about 0.005 millimeter ($\frac{1}{4800}$ of an inch) in diameter. The *cement* is much like bone in structure and composition, possessing lacunæ and canaliculi, but rarely any Haversian canals. It is thickest at the tip of the fang and thins away towards the cervix. *Enamel* is the hardest tissue in the Body, yielding on analysis only from two per cent to three per cent of organic matter, the rest being mainly calcium phosphate and carbonate. Its histological elements are minute hexagonal prisms, closely packed, and set on vertically to the surface of

the subjacent dentine.   It is thickest over the free end of the crown, until worn away by use.   Covering the enamel in

Fig. 110.—Section through a premolar tooth of the cat still imbedded in its socket.   1, enamel ; 2, dentine ; 3, cement ; 4, the gum ; 5, the bone of the lower jaw ; c, the pulp-cavity.

unworn teeth is a thin structureless horny layer, the *enamel cuticle.*

The **Tongue** (Fig. 111) is a muscular organ covered by mucous membrane, extremely mobile, and endowed not only with a delicate tactile sensibility but with the terminal organs of the special sense of taste; it is attached by its root to the hyoid bone.   On its upper surface are numerous small

eminences or *papillæ*, such as are found more highly developed on the tongue of a cat, where they may be readily felt. On the human tongue there are three forms of papillæ, the *circumvallate*, the *fungiform*, and the *filiform*. The circumvallate papillæ, 1 and 2, the largest and least numerous, are from seven to twelve in number and lie near the root of the tongue arranged in the form of a V with its open angle turned

1

Fɪɢ. 111.—The upper surface of the tongue with part of the pillars of the fauces and the tonsils. 1, 2, circumvallate papillæ ; 3, fungiform papillæ ; 4, filiform papillæ ; 6, mucous glands ; 7, tonsils ; 8, tip of epiglottis

forwards. Each is an elevation of the mucous membrane, covered by epithelium, and surrounded by a trench. On the sides of these papillæ, imbedded in the epithelium, are many small oval bodies richly supplied with nerves and sup-

posed to be concerned in the sense of taste, and hence called the *taste-buds* (Chap. XXXV). The *fungiform papillæ*, 3, are rounded elevations attached by somewhat narrowed stalks, and found all over the middle and fore part of the upper surface of the tongue. They are easily recognized on the living tongue by their bright red color. The *filiform papillæ*, most numerous and smallest, are scattered all over the dorsum of the tongue except near its base. Each is a conical eminence covered by a thick horny layer of epithelium. It is these papillæ which are so highly developed on the tongues of *Carnivora*, and serve them to scrape bones clean of even such tough structures as ligaments.

In health the surface of the tongue is moist, covered by little " fur," and in childhood of a red color. In adult life the natural color of the tongue is less red, except around the edges and tip; a bright-red glistening tongue being then, usually a symptom of disease. When the digestive organs are deranged the tongue is commonly covered with a thick yellowish coat, composed of a little mucus, some cells of epithelium shed from the surface, and numerous microscopic organisms known as bacteria; and there is frequently a " bad taste in the mouth." The whole alimentary mucous membrane is in close physiological relationship; and anything disordering the stomach is likely to produce a " furred tongue."

The Salivary Glands. The saliva, which is poured into the mouth and which, mixed with the secretion of minute glands imbedded in its lining membrane, moistens it, is secreted by three pairs of glands, the *parotid*, the *submaxillary* and the *sublingual*. The parotid glands lie in front of the ear behind the ramus of the lower jaw; each sends its secretion into the mouth by a tube known as *Stenon's duct*, which crosses the cheek and opens opposite the second upper molar tooth. In the disease known as *mumps* * the parotid glands are inflamed and enlarged. The submaxillary glands lie between the halves of the lower jaw-bone, near its angles, and their ducts open beneath the tongue near the middle line. The sublingual glands lie beneath the floor of the mouth, covered by its mucous membrane, between the back part of the tongue and the lower jaw-bone. Each has many ducts

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* *Parotitis,* in technical language.

(8 to 20), some of which join the submaxillary duct, while the rest open separately in the floor of the mouth.

The **Fauces** is the name given to the aperture which can be seen at the back of the mouth below the soft palate (Fig. 105), and leading into the pharynx. It is bounded above by the soft palate and uvula, below by the root of the tongue, and on the sides by muscular elevations covered by mucous membrane, which reach from the soft palate to the tongue. These elevations are the *pillars of the fauces.* Each bifurcates below, and in the hollow between its divisions lies a *tonsil* (7, Fig. 111), a soft rounded body about the size of an almond, and containing numerous minute glands which form mucus.

The tonsils not unfrequently become enlarged during a cold or sore throat, and then pressing on the Eustachian tube (Chap. XXXIV), which leads from the pharynx to the middle ear, keep it closed and produce partial deafness.

The **Pharynx or Throat-cavity** (Fig. 105). This portion of the alimentary canal may be described as a conical bag with its broad end turned upwards towards the base of the skull, and its narrow end downwards and passing into the gullet. Its front is imperfect, presenting openings which lead into the nose, the mouth, and (through the larynx and windpipe) the lungs. Except during swallowing or speech the soft palate hangs down between the mouth and pharynx; during deglutition it is raised into a horizontal position and separates an upper or *respiratory portion* of the pharynx from the rest. Through this upper part, therefore, air alone passes, entering it from the posterior ends of the two nostril-chambers; while through the lower portion both food and air pass, one on its way to the gullet, *b*, Fig. 105, the other through the larynx, *d*, to the windpipe, *c*; when a morsel of food " goes the wrong way " it takes the latter course. Opening into the upper portion of the pharynx on each side is an Eustachian tube, *g*: so that the apertures leading out of it are seven in number; the two posterior nares, the two Eustachian tubes, the fauces, the opening of the larynx, and that of the gullet. At the root of the tongue, over the opening of the larynx, is a plate of cartilage, the *epiglottis*, *e*, which can be seen if the mouth is widely opened and the back of the tongue pressed down by some such thing as the handle of a spoon. During swallowing the epiglottis

is pressed down like a lid over the air-tube and helps to keep food or saliva from entering it. In structure the pharynx consists essentially of a bag of connective tissue lined by mucous membrane, and having muscles in its walls which drive the food on.

The Œsophagus or **Gullet** is a tube commencing at the lower termination of the pharynx and which, passing on through the neck and chest, ends below the diaphragm by joining the stomach. In the neck it lies close behind the windpipe. It consists of three coats—a mucous membrane within; next, a submucous coat of areolar connective tissue: and, outside, a muscular coat made up of two layers, an inner with transversely and an outer with longitudinally arranged fibres. In and beneath its mucous membrane are numerous small mucous glands whose ducts open into the tube.

The Stomach (Fig. 112) is a somewhat conical bag placed transversely in the upper part of the abdominal cavity. Its larger end is turned to the left and lies close beneath the diaphragm; opening into its upper border, through the *cardiac orifice* at *a*, is the gullet *d*. The narrower right end is continuous at *c* with the small intestine; the aperture between the two is the *pyloric orifice*. The pyloric end of the stomach lies lower in the abdomen than the cardiac, and is separated from the

Fig. 112.—The stomach. *d*, lower end of the gullet ; *a*, position of the cardiac aperture ; *b*, the fundus ; *c*, the pylorus : *e*, the commencement of the small intestine ; along *a, b, c*, the great curvature ; between the pylorus and *d*, the lesser curvature.

diaphragm by the liver (see Fig. 1). The concave border between the two orifices is known as the *small curvature*, and the convex as the *great curvature*, of the stomach. From the latter hangs down a fold of peritoneum (*ne*, Fig. 1) known as the *great omentum*. It is spread over the rest of the abdominal contents like an apron. After middle life much fat frequently accumulates in the omentum, so that it is largely responsible for the "fair round belly with good capon lin'd." The protrusion *b* to the left side of the cardiac orifice, Fig. 112, is the *fundus* or great *cul de sac*. The size of the stomach varies greatly with the amount of food in it:

just after a moderate meal it is about ten inches long, by five wide at its broadest part.

Structure of the Stomach. This organ has four coats, known successively from without in as the serous, the muscular, the submucous, and the mucous. The *serous coat* is formed by a reflection of the peritoneum, a double fold of which slings the stomach; after separating to envelop it the two layers again unite and, hanging down beyond it, form the great omentum. The *muscular coat* (Fig. 59) consists of unstriped muscular tissue arranged in three layers: an outer, longitudinal, most developed about the curvatures; a circular, evenly spread over the whole organ, except around the pyloric orifice where it forms a thick ring; and an inner, oblique and very incomplete, radiating from the cardiac orifice. The *submucous coat* is made up of lax areolar tissue and binds loosely the mucous coat to the muscular. The *mucous coat* is a moist pink membrane which is inelastic, and large enough to line the stomach evenly when it is fully distended. Accordingly, when the organ is empty and shrunken, this coat is thrown into folds, which disappear when the organ is distended. During digestion the arteries supplying the stomach become dilated and, its capillaries being gorged, its mucous membrane is then much redder than during hunger.

The blood-vessels of the stomach run to it between the folds of *peritoneum* which sling it. After giving off a few branches to the outer layers, most of the arteries break up into small branches in the submucous coat, from which twigs proceed to supply the close capillary network of the mucous membrane.

The nerves of the stomach are chiefly derived from the pneumogastrics. In the lower part of the thorax these nerves consist mainly of nonmedullated fibres, and lie on the sides of the gullet, across which they interchange fibres by means of several branches. On entering the abdomen the left pneumogastric passes to the ventral side of the stomach, in which it ends: the right supplies the dorsal side of the stomach, but a considerable portion of it passes on to enter the *solar plexus*, which lies behind the stomach and contains several large ganglia. The sympathetic also supplies gastric nerves which mainly go to the blood-vessels. In the muscular coat of the stomach are many nerve-cells.

Histology of the Gastric Mucous Membrane. Examina-

tion of the inner surface of the stomach with a hand lens shows it to be covered with minute shallow pits. Into these open the mouths of minute tubes, the *gastric glands*, which are closely packed side by side in the mucous membrane; something like the cells of a honeycomb, except that each is open at one end. Between them lie a small amount of connective tissue, a close network of lymph-channels, and capillary blood-vessels. The connective tissue is of a peculiar variety closely packed with lymph-cells and will be more minutely described later (Chap. XXIII). The whole surface of the mucous membrane is lined by a single layer of columnar mucus-making epithelium cells (Fig. 113). These dip down and line the necks of the tubular glands. The deeper portions of the glands are lined by a layer of shorter and somewhat cuboidal cells, the *central* or *chief* cells. In specimens taken from a healthy animal killed during digestion these cells are large and do not stain deeply with carmine. Similar specimens taken from an animal an hour or two after a good meal has been swallowed show the *chief* cells shrunken and staining more deeply. They, thus, store up during rest a material which they get rid of when the gastric juice is being secreted. This material is, in part, *pepsinogen*, which during activity of the gland is changed, giving rise among other things to *pepsin*, the chief enzyme of gastric juice. The deeply staining protoplasmic portion of the cell which is left behind, forms and stores more pepsinogen during the next period during which the stomach is not digesting. In the pyloric end of the stomach only the chief cells line the glands, but elsewhere there is found outside them, in most of the glands, an incomplete layer of larger *oval* cells (*d*, Fig. 113). These are sometimes called the *oxyntic cells*, from the belief that they are especially concerned in secreting the acid of the gastric juice. The glands frequently branch at their deeper ends.

The Pylorus. If the stomach be opened it is seen that the mucous membrane projects in a fold around the pyloric

FIG. 113. — A thin section through the gastric mucous membrane, perpendicular to its surface, magnified about 25 diameters. *a*, a simple gastric gland ; *b*, a compound gastric gland ; *c*, a gland containing only *chief* cells ; *d*, oval or so-called *oxyntic* cells ; *o*, retiform connective tissue.

orifice and narrows it. This is due to a thick ring of the circular muscular layer there developed, and forming around the orifice a *sphincter muscle*, which, by its contraction, keeps the passage to the small intestine closed except when portions of food are to be passed on from the stomach to succeeding divisions of the alimentary canal.

Since the cardiac end of the stomach lies immediately beneath the diaphragm, which has the heart on its upper side, its over-distension, due to indigestion or flatulence, may impede the action of the thoracic organs, and cause feelings of oppression in the chest, or palpitation of the heart.

The Small Intestine (Fig. 120), commencing at the pylorus, ends, after many windings, in the large. It is about six meters (twenty feet) long, and about five centimeters (two inches) wide at its gastric end, narrowing to about two thirds of that width at its lower portion. Externally there are no lines of subdivision on the small intestine, but anatomists arbitrarily describe it as consisting of three parts; the first twelve inches being the *duodenum, D,* the succeeding two fifths of the remainder the *jejunum, J,* and the rest the *ileum, I.*

Like the stomach, the small intestine possesses four coats; a serous, a muscular, a submucous, and a mucous. The *serous coat* is formed by a duplicature of the peritoneum, but presents nothing answering to the great omentum; this double fold, slinging the intestine as the small omentum slings the stomach, is named the *mesentery.* The *muscular coat* is composed of plain muscular tissue arranged in two strata, an outer longitudinal, and an inner transverse or circular. The *submucous coat* is like that of the stomach; consisting of loose areolar tissue, binding together the mucous and muscular coats, and forming a bed in which the blood and lymphatic vessels (which reach the intestine in the fold of the mesentery) break up into minute branches before entering the mucous membrane.

The Mucous Coat of the Small Intestine. This is pink, soft and extremely vascular. It does not present temporary or effaceable folds like those of the stomach, but is, throughout a great portion of its length, raised up into permanent transverse folds in the form of crescentic ridges, each of which runs transversely for a greater or less way round the tube (Fig. 114). These folds are the *valvulæ conniventes.*

They are first found about two inches from the pylorus, and are most thickly set and largest in the upper half of the jejunum, in the lower half of which they become gradually less conspicuous; and they finally disappear altogether about the middle of the ileum. The folds serve greatly to increase the surface of the mucous membrane both for absorption and secretion, and they also delay the food somewhat in its passage, since it must collect in the hollows between them, and so be longer exposed to the action of the digestive liquids. Examined closely with the eye or, better, with aid of a lens, the mucous membrane of the small intestine is seen to be not smooth but shaggy, being covered everywhere (both over the valvulæ conniventes and between them) with closely packed minute processes, standing up somewhat like the "pile" on velvet, and known as the *villi.* Each villus is from 0.5 to 0.7 millimeter ($\frac{1}{50}$ to $\frac{1}{35}$ inch) in length; some are conical and rounded, but the majority are compressed at the base in one diameter (Fig. 115). In structure a villus is somewhat complex. Covering it is a single layer of columnar epithelial cells, the exposed ends of the majority having a peculiar bright striated border and being probably of great importance in absorption. Mixed with these cells are others in which most of the cell has become filled with a clear mass which does not stain readily with reagents; the deep narrow end of the cell stains easily and contains the nucleus. From time to time the clear substance (mucigen) is converted into mucus and discharged into the intestine, leaving behind only the nucleus and the protoplasm around it. These reconstruct the cell and form more mucigen. These mucus-forming cells are named *goblet-cells,* from their shape. Beneath the epithelium the villus may

Fig. 114.—A portion of the small intestine opened to show the *valvulæ conniventes.*

be regarded as made up of a framework of connective tissue, mainly of the adenoid variety (Chap. XXIII), supporting the

more essential constituents. Near the surface is an incomplete layer of plain muscular tissue, continuous below with a muscular stratum forming the deepest layer of the mucous membrane and named the *muscularis mucosæ*. In the centre is an offshoot of the lymphatic system; sometimes in the form of a single vessel with a closed dilated end, and sometimes as a network formed by two main vessels with cross-branches. During digestion these lymphatics are filled with a milky-white liquid absorbed from the intestines, and they are accordingly called the *lacteals*. They communicate with larger branches in the submucous coat, which end in trunks that pass out through the mesentery to join the main lymphatic system. Finally, in each villus, outside the lacteals and beneath the muscular layer of the villus, is a close network of blood-vessels.

Opening on the surface of the small intestine, between the bases of the villi, are small glands, the *crypts of Lieber·kühn*. Each is a simple unbranched tube lined by a layer of columnar cells some of which have a striated free border, though less marked than that on the corresponding cells of

Fig. 115.—Villi of the small intestine; magnified about 80 diameters. In the right-hand figure the lacteals, *a, b, c,* are filled with white injection; *d,* blood-vessels. In the left-hand figure the lacteals alone are represented, filled with a dark injection. The epithelium covering the villi, and their muscular fibres, are omitted.

the villi, and others are goblet-cells. The crypts of Lieber-kühn are closely packed, side by side, like the glands of the stomach. In the duodenum are found other minute glands, *the glands of Brunner*. They lie in the submucous coat

and send their ducts through the mucous membrane to open on its inner side.

The Large Intestine (Fig. 120), forming the final portion of the alimentary canal, is about 1.5 meters (5 feet) long, and varies in diameter from about 6 to 4 centimeters (2½ to 1½ inches). Anatomists describe it as consisting of the *cæcum* with the *vermiform appendix*, the *colon*, and the *rectum*. The small intestine does not open into the commencement of the large but into its side, some distance from its closed upper end, and the cæcum, *CC*, is that part of the large intestine which extends beyond the communication. From it projects the *vermiform appendix*, a narrow tube not thicker than a cedar pencil, and about 10 centimeters (4 inches) long. The colon commences on the right side of the abdominal cavity where the small intestine communicates with the large, runs up for some way on that side (*ascending colon, AC*), then crosses the middle line (*transverse colon, TC*) below the stomach, and turns down (*descending colon, DC*) on the left side and there makes an S-shaped bend known as the *sigmoid flexure, SF;* from this the *rectum, R,* the terminal straight portion of the intestine, proceeds to the anal opening, by which the alimentary canal communicates with the exterior. In structure the large intestine presents the same coats as the small. The external stratum of the muscular coat is not, however, developed uniformly around it, except on the rectum, but occurs in three bands separated by intervals in which it is wanting. These bands being shorter than the rest of the tube cause it to be puckered, or sacculated, between them. The mucous coat possesses no villi or valvulæ conniventes, but is usually thrown into effaceable folds, like those of the stomach but smaller. It contains numerous closely set glands much like the crypts of Lieberkühn of the small intestine.

The Ileo-colic Valve. Where the small intestine joins the large there is a valve, formed by two flaps of the mucous membrane sloping down into the colon, and so disposed as to allow matters to pass readily from the ileum into the large intestine but not the other way.

The Nerves of the Intestines. These, like those of the heart with which we shall later have to compare them physiologically, are *intrinsic* and *extrinsic*. The former are connected with small ganglia found abundantly on the

plexus of Auerbach which lies between the two muscular coats, and the *plexus of Meissner* found in the submucous coat. The extrinsic fibres proceed immediately from the gangliated *solar plexus* already referred to and from a similar *mesenteric plexus* which lies lower in the abdomen; except a few branches to the longitudinal muscular coat of the rectum which pass directly from some of the sacral spinal nerves. Some of the fibres distributed from the solar plexus are those running from the brain in the right pneumogastric, and probably also from the left, having crossed over to the left in branches joining the two. Others reach the solar plexus by means of the splanchnics and other nerves proceeding from the thoracic parts of the two sympathetic chains. These are partly vaso-constrictor fibres (Chap. XVIII.), but in part go to the muscular coats of the intestine. They may be traced back through the communicating branches from sympathetic ganglia to the corresponding spinal nerves and thence by the ventral nerve-roots into the spinal cord. The fibres passing to the intestines from the mesenteric plexus reach that plexus from the posterior thoracic and anterior lumbar sympathetic ganglia, and can also be tracked by experiment to the spinal cord.

The Liver. Besides the secretions formed by the glands imbedded in its walls, the small intestine receives those of two large glands, the *liver* and the *pancreas,* which lie in the abdominal cavity. The ducts of both open by a common aperture into the duodenum about 10 centimeters (4 inches) from the pylorus.

The *liver* is the largest gland in the Body, weighing from 1400 to 1700 grams (50 to 64 ounces). It is situated in the upper part of the abdominal cavity (*le, le'*, Fig. 1), rather more on the right than on the left side and immediately below the diaphragm, into the concavity of which its upper surface fits, and reaches across the middle line above the pyloric end of the stomach. It is of dark reddish-brown color, and of a soft friable texture. A deep fissure incompletely divides the organ into *right* and *left lobes,* of which the right is much the larger; on its under surface (Fig. 116) shallower grooves mark off several minor lobes. Its upper surface is smooth and convex. The vessels carrying blood to the liver are the *portal vein, Vp,* and the *hepatic artery;* both enter it at a fissure (*the portal fissure*) on its under side,

and there also a duct passes out from each half of the organ. The ducts unite to form the *hepatic duct, Dh*, which meets at an acute angle, the *cystic duct, Dc*, proceeding from the gall-bladder, *Vf*, a pear-shaped sac in which the bile, or gall, formed by the liver, accumulates when food is not being digested in the intestine. The *common bile-duct, Dch*,

FIG. 116.—The under surface of the liver. *d*, right, and *s*, left lobe; *Vh*, hepatic vein; *Vp*, portal vein; *Vc* vena cava inferior; *Dch*, common bile-duct; *Dc*, cystic duct; *Dh*, hepatic duct; *Vf*, gall-bladder.

formed by the union of the hepatic and cystic ducts, opens into the duodenum. The blood which enters the liver by the portal vein and hepatic artery passes out by the *hepatic veins, Vh*, which leave the posterior border of the organ close to the vertebral column, and there open into the inferior vena cava just before it passes up through the diaphragm.

The Structure of the Liver. On closely examining the surface of the liver, it will be seen to be marked out into small angular areas from one to two millimeters ($\frac{1}{25}$ to $\frac{1}{12}$ inch) in diameter. These are the outer sides of the superficial layer of a vast number of minute polygonal masses, or *lobules*, of which the liver is built up; similar areas are seen on the surface of any section made through the organ. Each lobule (Fig. 117) consists of a number of *hepatic cells* supported by a close network of capillaries; and is separated from neighboring lobules by connective tissue,

larger blood-vessels, and branches of the hepatic duct. The *hepatic cells* are the proper tissue elements of the liver, all the rest being subsidiary arrangements for their nutrition and protection. Each is polygonal, nucleated and very granular, and has a diameter of about .025 millimeter ($\frac{1}{1000}$ of an inch). In each lobule they are arranged in rows or strings, which form a network, in the meshes of which the blood-capillaries run. Covering the surface of the liver is a layer of the peritoneum, beneath which is a dense

FIG. 117.—A lobule of the liver, magnified, showing the hepatic cells radiately arranged around the central intralobular vein, and the lobular capillaries interlaced with them.

connective-tissue layer, forming the *capsule of Glisson*. At the portal fissure offsets from this capsule run in, and line canals, *the portal canals*, which are tunnelled through the organ. These, becoming smaller and smaller as they branch, finally become indistinguishable close to the ultimate lobules. From their walls and from the external capsule, connective-tissue partitions radiate in all directions through the liver and support its other parts. In each portal canal lie three vessels—a branch of the portal vein, a branch of the hepatic artery, and a branch of the hepatic duct; the division of the portal vein being much the largest of the three. These vessels break up as the portal canals do, and all end in minute branches around the lobules. The blood carried in by the portal vein (which has already circulated through the capillaries of the stomach, spleen, intestines and

pancreas) is thus conveyed to a fine vascular *interlobular plexus* around the liver-lobules, from which it flows on through the capillaries (*lobular plexus*) of the lobules themselves. These (Fig. 117) unite in the centre of the lobule to form a small *intralobular vein*, which carries the blood out and pours it into one of the branches of origin of the hepatic vein, called the *sublobular vein*. Each of the latter has many lobules emptying blood into it, and if dissected out with them (Fig. 118) would look something like a branch of a tree with apples attached to it by short stalks, represented

FIG. 118.—A small portion of the liver, injected, and magnified about twenty diameters. The blood vessels are represented white, the large vessel is a sublobular vein, receiving the intralobular veins, which in turn are derived from the capillaries of the lobules.

by the intralobular veins. The blood is finally carried, as already pointed out, by the hepatic veins into the inferior vena cava. The hepatic artery, a direct offshoot of the cœliac axis, ends mainly in Glisson's capsule and the walls of the blood-vessels and bile-ducts, but some of its blood reaches the lobular plexuses; it all finally leaves the liver by the hepatic veins.

The bile-ducts can be readily traced to the periphery of the lobules, and there communicate with a network of extremely minute commencing bile ducts, ramifying in the lobule between the hepatic cells composing it.

The Pancreas or Sweetbread. This is an elongated soft organ of a pinkish yellow color, lying along the great curvature of the stomach. Its right end is the larger, and is embraced by the duodenum (Fig. 119), which there

makes a curve to the left. A duct traverses the gland and joins the common bile-duct close to its intestinal opening. The pancreas produces a watery-looking secretion which is of great importance in digestion; the gland also (Chap. XXIII) exerts an important influence on the general nutritional processes of the Body. It is of the compound racemose type.

V   Lt

Fig. 119.—The stomach, pancreas, liver, and duodenum with part of the rest of the small intestine and the mesentery; the stomach and liver have been turned up so as to expose the pancreas. *V* stomach; *D, D', D''* duodenum; *L,* spleen; *P,* pancreas; *R,* right kidney; *T,* jejunum; *Vf,* gall-bladder; *h,* hepatic duct; *c,* cystic duct; *ch,* common bile-duct. 1, aorta; 2, an artery (left coronary) of the stomach; 3, hepatic artery; 4, splenic artery; 5, superior mesenteric artery; 6, superior mesenteric vein; 7, splenic vein; *Vp,* portal vein.

The Blood-vessels of Alimentary Canal, Liver, Spleen and Pancreas. The portal vein (*Vp,* Fig. 119) has already

been referred to as differing from all other veins in that it not only receives blood from a system of capillaries but ends in a second set of capillaries, which lie in the liver. The quantity of blood brought to supply the hepatic capillaries by the hepatic artery is in fact much less than that brought by the portal vein. The stomach, the intestines, the pancreas and the spleen are supplied with arterial blood from three great branches of the aorta. The most anterior of these, the *cœliac axis*, springs from the aorta close beneath the diaphragm and divides into the *hepatic artery, splenic artery*, and arteries for the stomach; some of these divisions may be seen in Fig. 119. The pancreas is supplied partly from the hepatic, partly from the splenic artery. The two other branches (*superior* and *inferior mesenteric artery*) are given off from the aorta lower down in the abdominal cavity; the former (5, Fig. 119) supplies the small intestine and half of the large, the latter the remainder of the large. The blood passing through all these arteries becomes venous in the capillaries of the organs they supply, and is gathered into corresponding veins (Fig. 119) which unite near the liver to form the portal vein. The further course of the blood carried to the liver (partly arterial from the hepatic artery, partly venous from the portal system) has been described already (p. 345).

Fig. 120.—Diagram of abdominal part of alimentary canal. *O*, the cardiac, and *P*, the pyloric end of the stomach; *D*, the duodenum; *J, I*, the convolutions of the small intestine; *CC*, the cæcum with the vermiform appendix; *AC*, ascending, *TC*, transverse, and *DC*, descending colon; *R*, the rectum

CHAPTER XXIII.

THE LYMPHATIC SYSTEM AND THE DUCTLESS GLANDS.

The **Lymphatics** or **Absorbents** are very widely distributed in the Body. Most organs, as has been pointed out (p. 63), possess a sort of internal skeleton made up of connective tissue, which consists mainly of bundles of fibres, united together and covered-in by a "cement" substance. In this substance are found numerous cavities, usually branched, and communicating with one another by their branches. They frequently contain connective-tissue corpuscles, which, however, do not completely fill them; and they thus, with their branches, form a set of intercommunicating channels known as the "*lymph-canaliculi,*" because they are filled with lymph. As the connective tissues accompany blood-vessels wherever the latter run, the canaliculi, which are frequently relatively large around the blood-capillaries, take up the liquid which transudes through their walls, and this *transudation liquid* is the origin of the lymph. Even where blood-vessels and connective tissue do not penetrate, as in bone between the Haversian canals, lymph-canaliculi penetrate, being connected with the cavities in which the bone-corpuscles lie; and in the deeper layers of the epidermis the cells are covered with prickle-like projections and unite by the tips of these so as to leave minute channels which apparently are lymph-canaliculi. These very minute channels, with no definite lining cells, but mere crevices between tissue elements, or tubes hollowed out in the matrix of connective tissue, bone and (possibly) cartilage, constitute the origin of the lymphatic system. The transudation liquid which enters them from the blood-vessels is rapidly altered by interchange with the neighboring tissues, losing certain materials and gathering others; and as the substances taken and the waste and other products returned vary very much in different organs, the lymph leaving them must differ also. Nevertheless it retains certain common features, histological

and chemical (pp. 49, 62), which justify us in speaking of it in general as *the lymph.* The lymphatic vessels collect this lymph or at least such part of it as does not pass back locally by diffusion into the blood, and pour it into the veins.

The Structure of Lymph-vessels. The smallest lymph-vessels proper are the *lymph-capillaries;* tubes rather wider than the blood-capillaries, but like them having a wall consisting of a single layer of flattened epithelium cells. The cells have, however, a wavy margin and are not as a rule much longer in one diameter than another, in both of which respects they differ from the cells of the corresponding blood-vessels. In some regions, as in many glands, the lymph-capillaries are much dilated and form irregular lymph *lacunæ,* everywhere bounded by their peculiar wavy cells, lying in the interstices of organs; and sometimes they form tubes around small blood-vessels, as in the brain (*perivascular lymph-channel*). In some places they commence by blind ends as in the lacteal vessels of the villi of the small intestine (Fig. 115) which are lymph-capillaries; but usually they branch and join to form networks. Lymph from the canaliculi enters them (whether by passing through their boundary cells or through clefts left between these is not certain) and is passed on to larger vessels which much resemble veins of corresponding size, having the same three coats, and being abundantly provided with valves.

The Thoracic Duct. The lymph-vessels proceeding from the capillaries in various organs become larger and fewer by joining together, and all end finally in two main trunks which open into the venous system on the sides of the neck, at the point of junction of the jugular and subclavian veins. The trunk on the right side is much smaller than the other and is known as the "*right lymphatic duct.*" It collects lymph from the right side of the thorax, from the right side of the head and neck, and the right arm. The lymph from all the rest of the Body is collected into the *thoracic duct.* It commences at the upper part of the abdominal cavity in a dilated reservoir (the *receptaculum chyli*), into which the lacteals from the intestines, and the lymphatics of the rest of the lower part of the Body, open. From thence the thoracic duct, receiving tributaries on its course, runs up the thorax alongside of the aorta and, passing on into the neck, ends on the left side at the point already indicated; receiving on its way the main stems from the left arm and the left side of the

head and neck. The thoracic duct, thus, brings back to the blood much more lymph than the right lymphatic duct.

The Serous Cavities. These are great dependencies of the lymphatic system and may be regarded as large lacunæ. Each of them (peritoneal, pleural, arachnoidal and pericardiac) is lined by a definite epithelioid layer of close-fitting polygonal cells. At certain points, however, openings or *stomata* occur, surrounded by a ring of smaller cells, and leading into tubes which open into subjacent lymphatic vessels. The liquid moistening these cavities is, then, really lymph: in some dropsical diseases it collects in great excess in them.

Lymphoid or Adenoid Tissue is the name given to certain aggregations of slightly differentiated cells (*leucocytes*) supported by a peculiar form of tissue and found in connection with the lymphatic system in many parts of the body. The cells much resemble white blood-corpuscles, though their nuclei usually have a more distinct network, and they are capable of executing amœboid movements. Many of them ultimately are carried by the lymph into the blood to become pale corpuscles, and from the blood some again pass back into the lymph by migrating through the walls of the blood-capillaries. By amœboid movement these lymph-corpuscles can take up foreign particles into themselves and creep with the absorbed material along lymph-canaliculi and lymph-capillaries. Lymphoid tissue is extensively developed in the mucous membrane of a great part of the alimentary canal.

The deepest layer of the mucous membrane of stomach and intestines, lying next to the submucous coat is the *muscularis mucosæ*, a thin layer of unstriped muscular tissue quite distinct from the proper muscular coats of those viscera. Above it and forming the main bulk of the mucous membrane lying between the glands (*o*, Fig. 112) and, in the small intestine, the main mass of the villi, is a delicate connective tissue consisting of very fine fibres which originated by the branching of cells; in many places the nuclei of these cells have quite disappeared, and the original central part of the cell is only recognizable as the place from which the branches spread: such tissue is reticular connective tissue. Its meshes contain many leucocytes, and the mixture of reticular tissue with these cells constitutes *adenoid* or *lymphoid tissue*. At numerous spots,

especially in the small intestine, the cells are peculiarly abundant, forming local aggregations of about the size of the head of a small pin: these are named *closed* or *solitary follicles*. A minute artery enters each and gives rise to a capillary network in it, from which the blood is carried off by a small vein. The follicle lies in, or rather projects into, a lymph-lacunæ which closely invests it, and is in direct communication with other lymphatic vessels of the neighborhood. The central leucocytes of the follicle are smaller than the outer, and their nuclei are often found in various stages of karyokinesis. Each follicle must therefore be regarded as a seat of formation of new leucocytes, new-made ones being pushed to the outside, growing, and finally being cast out into the surrounding lymph-lacuna, to be carried away in the lymph-current.

Near the lower part of the ileum large numbers of solitary follicles are closely collected side by side at intervals along the part of the bowel opposite to that at which the mesentery joins it: these aggregations are known as *Peyer's patches;* and are easily recognizable by the unaided eye, as villi are absent from the part of the mucous membrane opposite them, and they also cause a bulging, visible on the outside of the intestine. They disappear after middle life.

The Lymphatic Glands are essentially Peyer's patches more complicated in structure by the fact that the constituent follicles are more closely united and are gathered into roundish masses instead of being spread out in a single layer. They are found in various regions on the course of lymphatic vessels; especially in the mesentery, groin and neck. In the latter position they often inflame and give rise to abscesses, especially in tuberculous persons; and still more often enlarge, harden and become more or less tender, so as to attract attention to them. In common parlance it is then frequently said that the person's "kernels have come down," or that he has "waxing kernels." Each lymphatic gland is enveloped in a connective-tissue capsule, partitions of which incompletely divide it into chambers in which the lymphoid tissue lies. The partitions are more complete in the outer parts of the gland (*cortical portion*), which accordingly looks different from the central portion (*medulla*) in sections. In the lymphoid tissue are contained many leucocytes in process of division. "Afferent" lymphatic vessels open into the pe-

riphery of the gland, and efferent vessels arise in its centre. Hence the lymph in its flow traverses the cellular gland substance, and in its course picks up extra corpuscles which it carries on to the blood. In the lymphoid tissue there is a close network of blood-capillaries. It is clear that these organs are not true glands, in the proper sense of the word: they are sometimes called *lymphatic ganglia*, but that suggests a connection with nerve-centres; a good name for them is *lymphatic nodes*. In Fig. 120 is given a diagrammatic representation of a lymphatic node.

Fig. 121.—Diagram of cross-section of a lymphatic gland: *al*, afferent lymphatic vessels; *el*, efferent lymphatic vessel; *tr*, one of the connective-tissue bands subdividing the gland: *C* cortical portion: *M*, medullary portion. The leucocytes are represented only in a part of the right half of the figure, where they are seen, *lh*, to lie closely packed in the centre of a gland-chamber, while towards the walls of the chamber, *ls*, where they are naturally less closely packed, they have been washed away, as often happens in preparing a specimen, leaving the reticular supporting tissue conspicuous.

The Movement of the Lymph. This is no doubt somewhat irregular in the commencing vessels, but, on the whole, sets on to the larger trunks and through them to the veins. In many animals (as the frog) at points where the lymphatics communicate with the veins, there are found regularly contractile "lymph-hearts" which beat with a rhythm independent of that of the blood-heart, and pump the lymph into a vein. In the human Body, however, there are no such hearts, and the flow of the lymph is dependent on less definite arrangements. It seems to be maintained mainly by three things. (1) The pressure on the blood-plasma in the capillaries is greater than that in the great veins of the neck; hence any plasma filtered through the capillary-walls will be

under a pressure which will tend to make it flow to the venous termination of the thoracic or the right lymphatic duct. (2) On account of the numerous valves in the lymphatic vessels (which all only allow the lymph to flow past them to larger trunks) any movement compressing a lymph-vessel will cause an onward flow of its contents. The influence thus exerted is very important. If a tube be put in a large lymphatic, say at the top of the leg of an animal, it will be seen that the lymph only flows out very slowly while the animal is quiet; but as soon as it moves the leg the flow is greatly accelerated. (3) During each inspiration the pressure on the thoracic duct is less than that in the lymphatics in parts of the Body outside the thorax (see Chap. XXV). Accordingly, at that time, lymph is pressed, or, in common phrase, is "sucked," into the thoracic duct. During the succeeding expiration the pressure on the thoracic duct becomes greater again, and some of its contents are pressed out; but on account of the valves of the vessels which unite to form the duct, they can only go towards the veins of the neck.

During digestion, moreover, contractions of the villi press on the lymph or chyle within them and force it on; and in certain parts of the Body gravity, of course, aids the flow, though it will impede it in others.

The Ductless Glands—Spleen, Thyroid, Thymus, Pituitary Body, Suprarenals.—There are in the Body several organs of such considerable size and so constantly present in vertebrate animals that *a priori* they would seem to be of functional importance. Until quite recently, however, the functions of nearly all of them were quite problematical, although it has long been known that pathological changes in some of them were associated with grave conditions of general disease. Even yet their physiology is very incompletely known.

When we speak of a true gland we mean an organ that forms some definite secretion which it pours out in a separate form, but the organs we are about to consider have no secreting recesses and no ducts: nevertheless some of them undoubtedly make, and pass into the lymph and blood, substances of great importance to the healthy working of the Body. Some true glands indeed do this, quite apart from the manufacture of what is usually spoken of as their secretion. Why so large an organ as the liver should be set apart for the formation of so comparatively unimportant a digestive fluid as

the bile was long a puzzle. We now know that the chief use of the liver is connected with the storage and formation of carbohydrate materials (see Chap. XXIX), and that, quite apart from the use of bile in digestion or the elimination of part of the bile as waste, the liver exerts an essential influence on the whole normal nutritional processes of the Body. Again, in the pancreas we have an organ which forms a very important digestive secretion, and it might well be that this was its sole use in the economy. But when the pancreas is carefully removed from an animal great nutritional disturbances follow, as shown, among other things, by *diabetes,* i.e., the presence of sugar in the urine. Since the pancreatic secretion poured into the intestine by the gland duct has much to do with the digestion of starch and its conversion into sugar, it might be supposed that mere digestive disturbances due to its absence led to the diabetic and general changes. But this is not so. If a piece of living pancreas be transplanted from one animal to beneath the skin of another, and left until it has grown there, the pancreas of the second animal may be removed without causing diabetes. Moreover it is possible by injecting melted paraffin into the pancreatic duct of an animal not only to prevent the gland secretion from reaching the intestine, but to cause atrophy of the true gland-cells. Yet animals so treated do not become diabetic. It is then clear that there is some material necessary to health and quite distinct from pancreatic juice formed by pancreatic tissue and taken up from it by the circulating liquids. Scattered through the pancreas, and quite distinct from its proper gland tissue, are peculiar patches of cells very richly supplied with blood-vessels. Probably these cells are concerned in the antidiabetic function of the gland; but whether through special cells or not, the organ has an important *internal secretion* to blood and lymph, in addition to its external secretion to its duct. This fact may have a very wide bearing: it may be that all organs, or many organs, in addition to their more obvious functions, do, as the result of the chemical processes taking place in them, manufacture substances a supply of which, to lymph or blood, is required for the life or health of distant parts of the Body. The waste of one organ before its final conversion into carbon dioxide, water, or urea, for elimination from the system, may be a necessary food of another. It is, for example, quite possible that the kreatin formed in

muscles and passed from them to the circulating fluid is essential to the general health of the Body. There are, however, so many muscles that the removal of some of them, as when a limb is amputated, does not cut off the kreatin supply, and so disease does not result. When, on the other hand, an organ is unique, as the thyroid, or exists only in a single pair, as the suprarenals, then removal or extensive disease, by depriving the system of the peculiar internal secretion of the organ concerned or, possibly, from the accumulation within the blood of substances which it is the function of the missing part to absorb and destroy, may, often in fact does, lead to widespread nutritional changes, resulting in death.

The Spleen. This is an organ situated at the left end of the stomach (*L*, Fig. 110) and is about 170 grams (6 oz.) in weight. Its size is, however, very variable; it enlarges during digestion and shrinks after it until the next meal. In many fevers, especially in those of malarial nature, it also becomes enlarged, frequently to a very great extent, and this enlargement may become permanent, constituting the so-called " ague-cake." In color the spleen is dark red, but if cut across numerous white spots of about 1 mm. ($\frac{1}{25}$ inch) diameter are seen scattered over the surface of the section: it is very richly supplied with blood which is carried away by the splenic vein (7, Fig. 119) and poured into the portal vein. The spleen possesses on its exterior a connective-tissue capsule very rich in elastic fibres and giving off numerous bands (*trabeculæ*) which branch and interlace throughout the organ forming a spongy mass, in the spaces of which is contained a soft red *pulp* of peculiar structure. The arteries of the organ by frequent branching are reduced to almost capillary size, and these terminal twigs enter into the pulp, and there, losing all coats but the lining epithelium, assume the structure of capillaries. The cells forming the walls of these capillaries next separate from one another so as to leave clefts between them, and at the same time become irregularly branched and, joining by their branches, form a supporting framework or *reticulum* through the pulp, into which latter the blood is poured freely through the spaces between the cells. The main mass of the splenic pulp consists of red blood-corpuscles, some normal in appearance, some appearing partly broken down; mixed with these are some white corpuscles, and some larger colorless amœboid

cells in which are often found one or more red corpuscles which have apparently been swallowed by them. There are also many pigmented granules, some free and some within amœboid cells; they are apparently the débris of red corpuscles which have been broken down. In early life the splenic pulp also contains granular colorless cells within which red corpuscles are seen in the process of development. The whole histological structure of the adult pulp suggests that in it many red blood-corpuscles are finally destroyed, setting free hæmoglobin and other coloring matters derived from it. This breaking down of hæmoglobin must also give rise to proteids and substances derived from the chemical degradation of proteids, and the spleen is extremely rich in nitrogenous crystalline substances. The increase in size of the spleen during digestion, when the veins of the alimentary canal are pouring great quantities of blood laden with absorbed matters into the portal system, suggests that the spleen supplies things to the liver at that time which are of importance to it. There is reason to believe that the main coloring matter of the bile (*bilirubin*) is derived from the hæmoglobin of red corpuscles which have completed their life-period and been destroyed, and it may be that the spleen takes the first steps in the preparation of bilirubin for its elimination from the Body as a waste product. There still is, however, much doubt as to the real function of the spleen; it almost certainly plays an important part in the proteid metabolisms of the Body. Though so large an organ it is not essential; animals from whom it has been completely removed can live a long time in good health. The red marrow of spongy bone greatly resembles the splenic pulp in histological characters and may have similar functions and be able to entirely take the place of the spleen when the organ has been excised. The white spots seen on the cut surface of a spleen are sections of masses of adenoid tissue attached to the smaller splenic arteries and named *Malpighian corpuscles;* they resemble the closed follicles of the intestine in structure.

The Thyroid Body or Gland. This organ lies in the neck on the sides of the windpipe and consists usually of a right and a left lobe united by a narrow isthmus across the front of the air-tube. It is about thirty grams (two ounces) in weight; in the disease known as *goitre* it is greatly enlarged and its structure altered. The thyroid is dark red in

color and very vascular, richly supplied with nerves, and is subdivided by connective tissue into cavities or *alveoli*, the largest of which are just visible to the unaided eye. Each alveolus is lined by a single layer of cuboidal cells, and filled by a glairy fluid which appears to contain mucin.

The very abundant blood-supply of the thyroid suggests that it is the seat of important metabolic or chemical changes, and observation and experiment confirm this. Extensive disease of the thyroid leads to great changes in the general nutrition of the Body, ending in the condition named *myxodœma;* muciginous liquid collects in the connective tissues, nervous and muscular activity are much impaired, tremors and convulsions occur, and finally a semi-idiotic condition (*cretinism*) comes on and is followed by death if all the gland be diseased. Quite similar symptoms follow the complete removal of the thyroid body from animals, or from man for tumors; but if even a small part of healthy gland-tissue be left behind the symptoms do not occur. Moreover, if a portion óf living thyroid from one animal be grafted beneath the skin of another, the thyroid of the latter can be completely removed without influencing the general health. It would seem then that the gland is the place of formation of some substance essential to the healthy working of the Body, but that under ordinary conditions of life the whole organ is not required to produce the necessary minimum of this substance. This view is strengthened by the fact that in patients with thyroid disease and in animals deprived of the organ the symptoms of myxodœma may be relieved or removed by adding raw thyroid tissue to the food, or by subcutaneous injection of the expressed juice of a fresh gland. When injected into a healthy animal extract of thyroid causes arterial dilatation, and a lowering of blood pressure.

The Thymus. This is a temporary organ of unknown function. It has its greatest size in proportion to the whole weight of the Body a short time before birth. After birth it grows in absolute weight for some time, but then begins to dwindle away and has usually completely disappeared by the twelfth or fourteenth year. It lies in front of the windpipe in the lower part of the neck and the upper part of the thorax, and is the "neck" sweetbread of the butcher as distinguished from the true sweetbread or pancreas. The

thymus essentially consists of adenoid tissue, and is well supplied with blood-vessels and lymphatics.

The Pituitary Body (Fig. 75) is in part an offshoot of the brain, and probably that portion of it is, like the pineal body, a remnant of a once functionally important ancestral organ. The anterior lobe of the pituitary body, however, is derived in development from the pharynx, of which it is an embryonic outgrowth. This part of it somewhat resembles the thyroid in structure. Complete removal of the pituitary body in the case of cats and dogs causes a lowering of temperature, muscular twitchings and spasms, difficulty in breathing, general lassitude, and death within a fortnight. These symptoms improve when extract of the gland is injected. The organ has therefore been supposed to form an internal secretion useful in maintaining the nutrition of the muscular and nervous systems. Disease of the pituitary body in man has been found to be associated with the curious condition named *acromegaly,* in which there is hypertrophy of the bones of the limbs and face, and of parts of the skin and mucous membranes. Injection of the extract of the gland causes, in a normal animal, a more powerful but not quicker heart-beat, and constriction of the arteries.

The Suprarenal Capsules or Adrenals are a pair of small organs, weighing together about 12 grams (⅔ oz.) placed one on the top of each kidney. They have, however, no intimate connection with the kidneys, and in many animals are placed at some distance from them. Each consists of a denser less colored external *cortex,* and a central deep yellow-brown softer *medulla.* The cortex is subdivided into chambers by connective tissue, and the chambers are filled by closely packed, polygonal nucleated cells. Similar cells are found in the medulla, which is, moreover, closely connected with the sympathetic system and is richly supplied with nerves.

It was noticed some fifty years ago by a physician named Addison that certain obscure diseased conditions characterized by great debility and by the appearance of bronzed patches on the skin, and leading to death, were found on post-mortem examination to be accompanied by disease of the adrenals. The disease has hence been named Addison's disease. When the suprarenal capsules are completely removed from animals a similar fatal diseased condition results, death taking place in warm-blooded animals within two or three days, and be-

ing preceded by muscular weakness, dilatation of the arteries, mental feebleness and general prostration. The exact rôle played in the organism by these small but essential organs is still unknown, but they form substances which have a profound effect on the nerves of the heart and blood-vessels. A very minute portion of the watery or alcoholic extract of a suprarenal capsule when injected into a vein of an animal causes a very slow heart-beat, or even complete inhibition of the auricles. If the cardio-inhibitory nerves have first been cut, on the other hand, the injection causes a great increase in the rate of heart-beat and a great increase of its force, especially that of the auricles. The small arteries become greatly contracted, and this combined with the powerful heart-beats leads to a very great increase of arterial pressure. The arterial constriction is not due to stimulation of the vaso-constrictor centre, but to a direct action on the muscular coats of the arteries: it is very transient. The skeletal muscles are also affected, the period of a simple muscular contraction being greatly prolonged, and this effect lasts much longer than the changes produced in the organs of circulation. The active material exists only in the medulla of the adrenal, is efficient in extremely minute doses, is dialyzable, and its efficacy is not impaired by short boiling.

It would appear then that the suprarenals are constantly forming and passing into the blood minute quantities of a substance which is of great importance for the maintenance of the "tone" of the muscles, especially of the cardiac and arterial muscles. Whether in addition they also remove noxious substances from the blood, the accumulation of which after their removal is one cause of the death which results, is still undecided. The blood of such animals acts as a poison to other animals, and this has been supposed to be due to the presence in it of a specific poison which the adrenals normally pick up and destroy: but it is clear that the blood of an animal dying from extensive malnutrition produced in any way would be quite abnormal, and might well be poisonous to other animals. The same remark may be made as to the poisonous character of the blood of animals dying as a result of removal of the thyroid: there is no satisfactory evidence that it is due to the accumulation of any one special toxic substance which it is a function of the thyroid to remove: still, it may be. The symptoms produced by its injection are quite different from those produced by injection of thyroid extract.

CHAPTER XXIV.

DIGESTION.

The Object of Digestion. Of the various foodstuffs swallowed, some are already in solution and ready to dialyze at once into the lymphatics and blood-vessels of the alimentary canal; others, such as a lump of sugar, though not dissolved when put into the mouth, are readily soluble in the liquids found in the alimentary canal, and need no further digestion. In the case of many most important foodstuffs, however, special chemical changes have to be wrought, either with the object of converting insoluble bodies into soluble, or nondialyzable into dialyzable, or both. The different secretions poured into the alimentary tube act in various ways upon different foodstuffs, and at last get them into a state in which they can pass into the circulating medium and be carried to all parts of the Body.

The Saliva. The first solvent that the food meets with is the saliva, which, as found in the mouth, is a mixture of pure saliva, formed in parotid, submaxillary, and sublingual glands, with the mucus secreted by small glands of the buccal mucous membrane. This *mixed saliva* is a colorless, cloudy, feebly alkaline liquid, "ropy" from the mucin present in it, and usually containing air-bubbles. Pure saliva, as obtained by putting a fine tube in the duct of one of the salivary glands, is more fluid and contains no imprisoned air.

Usually but little saliva is secreted ; the presence of food in the mouth, especially highly flavored or acid food, leads to a more abundant flow : the mere chewing of a tasteless inert substance will, however, excite some secretion. The secretion thus brought about is reflex: the afferent fibres running to the brain in the glossopharyngeal and lingual nerves, and exciting there the centre from which the efferent secretory nerve-fibres for the glands arise. The centre may be excited in other ways: as by nausea, or through the nerves of eye or nose when the sight or smell of desirable food makes " the mouth water."

The uses of the saliva are for the most part physical and mechanical. It keeps the mouth moist and allows us to speak with comfort; most young orators know the distress occasioned by the suppression of the salivary secretion through nervousness. and the imperfect efficacy under such circumstances of the traditional glass of water placed beside public speakers. The saliva, also, enables us to swallow dry food; such a thing as a cracker when chewed would give rise merely to a heap of dust, impossible to swallow, were not the mouth cavity kept moist. This fact used to be taken advantage of in the East Indian rice ordeal for the detection of criminals. The guilty person, believing firmly that he cannot swallow the parched rice given him, and fearful of detection, is apt to have the nerve-centres of his salivary glands inhibited or paralyzed by terror, and does actually become unable to swallow the rice; while in those with clear consciences the nervous system excites the usual reflex secretion, and the dry food gives rise to no difficulty in its deglutition. The saliva, also, dissolves such bodies as salt and sugar, when they are taken into the mouth in solid form, and enables us to taste them; undissolved substances are not tasted, a fact which any one can verify for himself by wiping his tongue dry and placing a fragment of sugar upon it. No sweetness will be felt until a little moisture has exuded and dissolved part of the sugar.

In addition to such actions the saliva, however, exerts a chemical one on an important foodstuff. Starch (although it swells up greatly in hot water) is insoluble, and could not be absorbed from the alimentary canal. The saliva contains an enzyme, *ptyalin*, which has the power of turning starch into soluble substances. Until recently the chief product was believed to be grape sugar (*glucose*); but it is now ascertained that it is maltose, belonging to the cane-sugar chemical series. In the small intestine the maltose is changed into glucose and absorbed; so the chemical action of ptyalin upon starch is at most but a preparatory one. In effecting the change the ptyalin is not altered; a very small amount of it can convert a vast amount of starch, and does not seem to have its activity impaired in the process. The starch is made to combine with the elements of one or more molecules of water, and the ptyalin is unchanged.

This faculty of ptyalin is known as *amylolytic:* and since

it is associated with the taking up of a molecule of water is a *hydrolytic action.* Ptyalin is a typical *enzyme;* it differs from the true ferments, such as yeast, in the fact that it is not a living organism, and does not multiply during the occurrence of the change which it sets up; its activity belongs to the obscure chemical category of *contact actions.*

In order that the ptyalin may act upon starch certain conditions are essential. Water must be present, and the liquid must be neutral or feebly alkaline; acids retard, or if stronger, entirely stop the process. The change takes place most quickly at about the temperature of the human Body, and is greatly checked by cold. Boiling the saliva destroys its ptyalin and renders it quite incapable of converting starch. Cooked starch is changed more rapidly and completely than raw.

Saliva has another important but indirect influence in promoting digestion. Weak alkalies stimulate the mucous membrane of the stomach and cause it to pour forth more gastric juice. Hence the efficacy of a little carbonate of soda, taken before meals, in some forms of dyspepsia. The saliva by its alkalinity exerts such an action; and this is one reason why food should be well chewed before being swallowed; for then its taste, and the movements of the jaws, cause the secretion of more saliva.

Deglutition. A mouthful of solid food is broken up by the teeth, and rolled about the mouth by the tongue, until it is thoroughly mixed with saliva and made into a soft pasty mass. The muscles of the cheeks keep this from getting between them and the gums; persons with facial paralysis have, from time to time, to press out with the finger food which has collected outside the gums, where it can neither be chewed nor swallowed. The mass is finally sent on from the mouth to the stomach by the process of *deglutition,* which is described as occurring in three stages. The first stage includes the passage from the mouth into the pharynx. The food being collected into a heap on the tongue, the tip of that organ is placed against the front of the hard palate, and then the rest of the tongue is raised from before back, so as to press the food mass between it and the palate, and drive it back through the fauces. This portion of the act of swallowing is voluntary, or at least is under the control of the will, although it commonly takes place unconsciously. The second

stage of deglutition is that in which the food passes through the pharynx; it is the most rapid part of its progress, since the pharynx has to be emptied quickly so as to clear the opening of the air-passages for breathing purposes. The food mass, passing back over the root of the tongue, pushes down the epiglottis; at the same time the larynx (or voice-box at the top of the windpipe) is raised, so as to meet it, and thus the passage to the lungs is closed ; muscles around the aperture probably also contract and narrow the opening. The raising of the larynx can be readily felt by placing the finger on the large cartilage forming "Adam's apple" in the neck, and then swallowing something. The soft palate is at the same time raised and stretched horizontally across the pharynx, thus cutting off communication with its upper, or respiratory portion, leading to the nostrils and Eustachian tubes. Finally, the isthmus of the fauces is closed as soon as the food has passed through, by the contraction of the muscles on its sides and the elevation of the root of the tongue. All passages out of the pharynx except the gullet are thus blocked, and when the pharyngeal muscles contract the food can be squeezed only into the œsophagus. The muscular movements concerned in this part of deglutition are all reflexly excited; food coming in contact with the mucous membrane of the pharynx stimulates afferent nerve-fibres in it; these excite the *centre of deglutition* which is placed in the *medulla oblongata,* and from it efferent nerve-fibres proceed to the muscles concerned and (under the co-ordinating influence of the centre) cause them to contract in proper sequence. The pharyngeal muscles, although of the striped variety, are but little under the control of the will; it is extremely difficult to go through the movements of swallowing without something (if only a little saliva) to swallow and thus excite the movements reflexly. Many persons, after having got the mouth completely empty cannot perform the movements of the second stage of deglutition at all. On account of the reflex nature of the contractions of the pharynx, any food which has once entered it must be swallowed: the isthmus of the fauces is a sort of Rubicon; food that has passed it must continue its course to the stomach, although the swallower learnt immediately that he was taking poison. The third stage of deglutition is that in which the food is passing along the gullet, and is comparatively slow. Even liquid substances

do not fall or flow down this tube, but have their passage controlled by its muscular coats, which grip the successive portions swallowed and pass them on. Hence the possibility of performing the apparently wonderful feat of drinking a glass of water while standing upon the head, often exhibited by jugglers; the onlookers forget that the same thing is done every day by horses, and other animals, which drink with the pharyngeal end of the gullet lower than the stomach. The movements of the œsophagus are of the kind known as *vermicular* or *peristaltic*. Its circular muscular fibres contract behind the morsel and narrow the passage there; and the constriction then travels along to the stomach, pushing the food in front of it. Simultaneously the longitudinal fibres, at the point where the food-mass is at any moment and immediately in front of that, contracting, shorten and widen the passage.

The Gastric Juice.—The food having entered the stomach is subjected to the action of the gastric juice, which is a thin, colorless or pale yellow liquid, of a strongly acid reaction. It contains as specific elements *free hydrochloric acid* (about .2 per cent), and an enzyme called *pepsin* which, in acid liquids, has the power of converting the ordinary non-dialyzable proteids which we eat, into closely allied bodies, some of which are dialyzable and named *peptones*. It also dissolves solid proteids, changing them similarly. Dilute acids will by themselves produce the same changes in the course of several days, but in the presence of pepsin and at the temperature of the Body the conversion is far more rapid. In neutral or alkaline media the pepsin is inactive; and cold checks its activity. Boiling destroys it. In addition to pepsin, gastric juice contains another enzyme (*rennin*) which coagulates the caseinogen of milk, as illustrated by the use of "rennet," prepared from the mucous membrane of the calf's digestive stomach, in cheese-making. The acid of the natural gastric juice would, it is true, precipitate the casein, but such precipitate is quite different from the true tyrein, and neutralized gastric juice still possesses this power; moreover, boiled gastric juice loses the milk-clotting property, and a very little normal juice can coagulate a great quantity of milk. The curdled condition of the milk regurgitated by infants is, therefore, not any sign of a disordered state of the stomach, as nurses commonly suppose. It is proper for milk

to undergo this change, before the pepsin and acid of the gastric juice digest it.

The most important change effected by the gastric juice is that of the proteids. This may be studied either on natural juice obtained from the stomach of an animal through an opening (gastric fistula) or on an artificial juice prepared by extracting the mucous membrane of a fresh stomach with glycerine, and adding a large quantity of dilute (0.2%) hydrochloric acid. If blood-fibrin or boiled white of egg be placed in such a mixture and kept at a temperature of about 38° C. (100° F.) these bodies swell, become transparent, and soon dissolve; and all other solid proteids undergo similar changes. If the solution be now neutralized a small white precipitate of *parapeptone* (which is probably only ordinary acid albumin) is obtained. The filtrate from this gives no precipitate on boiling, but an abundant one of *albumose* on the addition of ammonium sulphate. The filtrate from this precipitate yields an abundant precipitate of *peptone* when alcohol is added. Peptone is dialyzable, though not so easily as saline bodies, and in this differs from albumose and parapeptone and all other proteids. The parapeptone is probably a bye-product due to the action of the acid of the juice alone: the albumose and peptone are true products of peptic digestion of proteids, due to their breaking up with concomitant hydration, the peptone being the more finished or complete digestive product. If instead of solid proteids we use solution of white of egg or of serum albumin, the earlier stages of the process cannot be followed by the eye, but the final products are the same: the original proteid disappears, giving origin to some parapeptone, to albumose, and to peptone; and prolonged artificial peptic digestion causes no further breaking up of the albumose or peptone. Peptone is very soluble in water, and its solutions are not coagulated by boiling. A very small amount of pepsin can, if some acid be added from time to time, convert a very large amount of proteid: it is destroyed by boiling.

Gastric Digestion. The process of swallowing is continuous, but in the stomach the onward progress of the food is stayed for some time. The pyloric sphincter, remaining contracted, closes the aperture leading into the intestine, and the irregularly disposed muscular layers of the stomach keep its semi-liquid contents in constant movement, maintaining a

sort of churning by which all portions are brought into contact with the mucous membrane, and thoroughly mixed with the secretion of its glands. The gelatin-yielding connective tissue of meats is dissolved away, and the proteid-containing fibres, left loose, are dissolved and changed. The albuminous walls of the fat-cells are dissolved and their oily contents set free; but the gastric juice does not act upon the latter. Certain mineral salts (as phosphate of lime, of which there is always some in bread) which are insoluble in water but soluble in dilute acids, are also dissolved in the stomach. On the other hand, the gastric juice has itself no action upon starch, and since ptyalin does not act at all, or only imperfectly, in an acid medium, the activity of the saliva in converting starch is stayed in the stomach. By the solution of the white fibrous connective tissue, that disintegration of animal foods commenced by the teeth, is carried much farther in the stomach, and the food-mass, mixed with much gastric secretion, becomes reduced to the consistency of a thick soup, usually of a grayish color. In this state it is called *chyme.* Chyme contains, after an ordinary meal, much peptone, though some of this has been already dialyzed into the gastric mucous membrane and carried off along with other dissolved dialyzable bodies, such as salts and sugar. The albumose, fats, and starch still remain in the chyme. After the food has remained in the stomach some time (one and a half to two hours) the chyme begins to be passed on into the intestine in successive portions. The pyloric sphincter relaxes at intervals, and the rest of the stomach, contracting at the same moment, injects a quantity of chyme into the duodenum; this is repeated frequently, the larger undigested fragments being at first unable to pass the orifice. At the end of about three or four hours after a meal the stomach is again quite emptied, the pyloric sphincter finally relaxing to a greater extent and allowing any larger indigestible masses, which the gastric juice cannot break down, to be driven into the intestine.

The Chyle. When the chyme passes into the duodenum it finds preparation made for it. The pancreas is in reflex connection with the stomach, and its nerves cause it to commence secreting as soon as food enters the latter; hence a quantity of its secretion is already accumulated in the intestine when food enters. The gall-bladder is distended with

bile, secreted since the last meal; this passing down the hepatic duct has been turned back up the cystic duct (*Dc,* Fig. 115) on account of the closure of the common bile-duct. The acid chyme, stimulating nerve-endings in the duodenal mucous membrane, causes reflex contraction of the muscular coat of the gall-bladder, and a relaxation of the orifice of the common bile-duct; and so a gush of bile is poured out on the chyme. From this time on, both liver and pancreas continue secreting actively for some hours, and pour their products into the intestine. The glands of Brunner and the crypts of Lieberkühn are also set at work, but concerning their physiology we know very little. All of these secretions are alkaline, and they suffice very soon to more than neutralize the acidity of the gastric juice, and to convert the acid *chyme* into alkaline *chyle,* which, after an ordinary meal, will contain a great variety of things: mucus derived from the alimentary canal; ptyalin from the saliva; pepsin from the stomach; water, partly swallowed and partly derived from the salivary and other secretions; the peculiar constituents of the bile and pancreatic juice and of the intestinal secretions; some undigested proteids; unchanged starch; oils from the fats eaten; peptones formed in the stomach but not yet absorbed; albumose; parapeptone; possibly salines and sugar which have also escaped absorption in the stomach; and indigestible substances taken with the food.

The Pancreatic Secretion is clear, watery, alkaline, and much like saliva in appearance. The Germans call the pancreas the "abdominal salivary gland." In digestive properties, however, the pancreatic secretion is far more important than the saliva, or even the gastric juice. Starch it changes as the saliva does, but converts it into maltose more quickly: and it acts also on proteids and fats. It is by far the most important of all the digestive secretions. All proteids not already converted into peptone or albumose are acted upon by the pancreatic juice even more energetically than in the stomach, being not only converted into peptone, but in part further broken up, if the digestion (artificial) be prolonged, and converted into crystallizable nitrogenous bodies which, unlike peptone, retain no proteid-like characters: the chief of these are *leucin* and *tyrosin,* the former allied chemically to the fatty acids, the other to bodies of the aromatic series. In normal digestion, however, it is

probable that but little of the proteid is broken up beyond the peptone stage, and all of it never is; an albumose is formed as an intermediate product. The enzyme concerned is *trypsin ;* it is active only in an alkaline or neutral medium, and before dissolving solid proteids does not cause them to swell and become transparent as pepsin does. Like the other digestive ferments, it is most active at about the temperature of the Body, and is destroyed by boiling. On fats the pancreatic secretion has a double action. To a certain extent it breaks them up, with hydration, into free fatty acids and glycerin; for example—

$$\left.\begin{matrix} (C_{18}H_{35}O)_3 \\ C_3H_5 \end{matrix}\right\} O_3 + 3H_2O = 3\left(\left.\begin{matrix} C_{18}H_{35}O \\ H \end{matrix}\right\} O\right) + \left.\begin{matrix} C_3H_5 \\ H_3 \end{matrix}\right\} O_3.$$

| 1 Stearin | + | 3 Water | = | 3 Stearic acid | + | 1 Glycerine. |
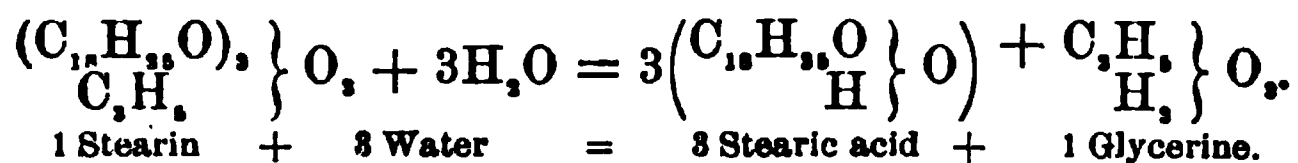
The fatty acid then combines with some of the alkali present to make a *soap*, which being soluble in water is capable of absorption. Glycerin, also, is soluble in water and dialyzable. The greater part of the fats are not, however, so broken up, but are simply mechanically separated into droplets, which remain suspended in the chyle and give it a whitish color, just as the cream-drops are suspended in milk, or the olive-oil in mayonnaise sauce. This is effected by the help of a quantity of albumin which exists dissolved in the pancreatic secretion. In the stomach, the animal fats eaten have lost their cell-walls, and have become melted by the temperature to which they were exposed. Hence their oily part floats free in the chyme when it enters the duodenum. If oil be shaken up with water, the two cannot be got to mix; immediately the shaking ceases, the oil floats up to the top; but if some raw egg be added, a creamy mixture is readily formed, in which the oil remains for a long time evenly suspended in the watery menstruem. The reason of this is that each oil-droplet becomes surrounded by a delicate pellicle of albumin, and is thus prevented from fusing with its neighbors to make large drops, which would soon float to the top. Such a mixture is called an *emulsion*, and the albumin of the pancreatic secretion emulsifies the oils in the chyle, which becomes white (for the same reason as milk is that color) because the innumerable tiny oil-drops floating in it reflect all the light which falls on its surface.

In brief, the pancreatic secretion converts starch into

maltose ; dissolves proteids (if necessary) and converts them into peptones; emulsifies fats, and, to a certain extent, breaks them up into glycerin and fatty acids; the latter are then saponified by the alkalies present.

The Bile.—Human bile when quite fresh is a golden brown liquid; it becomes green when kept. As formed in the liver it contains hardly any mucin, but if it make any stay in the gall-bladder it acquires much from the lining membrane of that bag, and becomes slimy and "ropy." It is alkaline in reaction and, besides coloring matters (the more important of which, *bilirubin*, is probably a waste product derived from hæmoglobin), contains mineral salts and water, and the sodium salts of two nitrogenized acids, *taurocholic* and *glychocholic*, the former predominating in human bile.

Pettenkofer's Bile Test. If a small fragment of cane sugar be added to some bile, and then a large quantity of strong sulphuric acid, a brilliant purple color is developed, by certain products of the decomposition of the bile acids; the physician can by this test, in disease, detect their presence in the urine or other secretions of the Body. *Gmelin's Bile Test.* The bile-coloring matters, treated with yellow nitric acid, go through a series of oxidations, accompanied with changes of color from yellow-brown to green, then to blue, violet, purple, red, and dirty yellow.

Bile has no digestive action upon starch or proteids. It does not break up fats, but to a limited extent emulsifies them, though far less perfectly than the pancreatic secretion. It is even doubtful whether this action is exerted in the intestines at all. In many animals, as in man, the bile and pancreatic ducts open together into the duodenum, so that, on killing a dog during digestion and finding emulsified fats in the chyle, it is impossible to say whether or no the bile had a share in the process. In the rabbit, however, the pancreatic duct opens into the intestine about a foot farther from the stomach than the bile-duct, and it is found that if a rabbit be killed after being fed with oil, no milky chyle is found down to the point where the pancreatic duct opens. In this animal, therefore, the bile alone does not emulsify fats, and, since the bile is pretty much the same in it and other mammals, it probably does not emulsify fats in them either. From the inertness of bile with respect to most food-stuffs it has been doubted whether it be of any digestive use at

all, and whether it should not be regarded merely as an excretion, poured into the alimentary canal to be got rid of. But there are many reasons against such a view. In the first place, the entry of the bile into the upper end of the small intestine where it has to traverse a course of more than twenty feet before getting out of the Body, instead of its being sent into the rectum, close to the final opening of the alimentary canal, makes it probable that it has some function to fulfil in the intestine. Moreover, a great part of the bile, including practically all the bile salts, poured into the intestines is again absorbed from them ; this seems to show that part of the bile is secreted for some other purpose than mere elimination from the Body. One subsidiary use is to assist, by its alkalinity, in overcoming the acidity of the chyme, and so to allow the trypsin of the pancreatic secretion to act upon proteids. Constipation is, also, apt to occur in cases where the bile-duct is temporarily stopped, so that bile probably helps to excite the contractions of the muscular coats of the intestine; under similar circumstances putrefactive decompositions are apt to occur in the intestinal contents. Apart from such secondary influences, however, the bile probably has some influence in promoting the absorption of fats. If one end of a capillary glass tube, moistened with water, be dipped in oil, the latter will not ascend in it, or but a short way; but if the tube be moistened with bile, instead of water, the oil will ascend higher in it. So, too, oil passes through a plug of porous clay kept moist with bile, under a much lower pressure than through one wet with water. Hence bile, by soaking the epithelial cells lining the intestine, may facilitate the passage into the villi of oily substances. At any rate, experiment shows that if the bile be prevented from entering the intestine of a dog, the animal eats an enormous amount of food compared with that amount which it needed previously; and that of this food a great proportion of the fatty parts passes out of the alimentary canal unabsorbed. There is no doubt, therefore, that the bile somehow aids in the absorption of fats, but exactly how is uncertain. Its possible action in exciting the muscles of the villi to contract will be referred to presently.

The Intestinal Secretions or Succus Entericus. These consist of the secretions of the glands of Brunner and the crypts of Lieberkühn. It is difficult to obtain them pure; indeed the product of Brunner's glands has never been obtained

unmixed. That of the crypts of Lieberkühn is watery and alkaline, and poured out more abundantly during digestion than at other times. It has no special action on starches, most proteids, or on fats; but is said to dissolve blood fibrin and convert it into peptone, and it changes maltose into grape sugar; so that this cane sugar is turned into a grape sugar before being absorbed. Mucus is also formed and poured out abundantly by the epithelium cells of the intestinal lining membrane. It is more especially secreted during fasting, and by its stickiness collects débris and keeps the mucous membrane clean.

Intestinal Digestion. Having considered separately the actions of the secretions which the food meets with in the small intestine we may now consider their combined effect.

The neutralization of the chyme, followed by its conversion into alkaline chyle, will prevent any further action of the pepsin on proteids, but will allow the ptyalin of the saliva (the activity of which was stopped by the acidity of the gastric juice) to recommence its action upon starch. Moreover, in the stomach there is produced, alongside of the albumose and true peptone, the parapeptone, which agrees very closely with syntonin in its properties, and this passes into the duodenum in the chyme. As soon as the bile meets the chyme it precipitates the parapeptone, and this carries down with it any peptones which, having escaped absorption in the stomach, may be present; it also precipitates the pepsin. In consequence, one finds in an animal killed during digestion, a granular precipitate over the villi, and in the folds between the valvulæ conniventes of the duodenum. This is redissolved by the pancreatic secretion, which also changes into peptone the proteids (usually a considerable proportion of those eaten at a meal) which have passed through the stomach unchanged, or as albumose or parapeptone. The conversion of starch into maltose will go on very rapidly under the influence of the pancreatic secretion. Fats will be split up and saponified to a certain extent, but a far larger proportion will be emulsified and give the chyle a whitish appearance. Later cane sugar, which may have escaped absorption in the stomach, and maltose will be converted into grape sugar and absorbed, along with such salines as may, also, have hitherto escaped. Elastic tissue from animal substances eaten,

cellulose from plants, and mucin from the secretions of the alimentary tract, will all remain unchanged.

Absorption from the Small Intestine. The chyme leaving the stomach is a semi-liquid mass which, mixed in the duodenum with considerable quantities of pancreatic secretion and bile, is further diluted. Thenceforth it gets the intestinal secretion added to it, but the absorption more than counterbalancing the addition of liquid, the food-mass becomes more and more solid as it approaches the ileo-colic valve. At the same time it becomes poorer in nutritive constituents, these being gradually removed from it in its progress; most dialyze through the epithelium into the subjacent blood and lymphatic vessels, and are carried off. Those passing into the blood capillaries are taken by the portal vein to the liver; while those entering the lacteals are carried into the left jugular vein by the thoracic duct. As to which foodstuffs go one road and which the other, there is still much doubt; sugars probably go by the portal system, while the fats, mainly, if not entirely, go through the lacteals. How the fats are absorbed is not clear, since oils will not dialyze through membranes, such as that lining the intestine, moistened with watery liquids. Most of them, nevertheless, get into the lacteals as oils and not as soluble soaps; for one finds these vessels, in a digesting animal, filled with white milky chyle; while at other periods their contents are watery and colorless like the lymph elsewhere in the Body. The little fat-drops of the emulsion formed in the intestine, go through the epithelial cells and not between them, for during digestion these cells are loaded with oil-droplets; as their free ends are striated and probably devoid of any definite cell-wall, it is possible that the intestinal movements squeeze oil-drops into them, but the cells may play a more active part. The striation of the border is due to closely-set rods which are known to be able to change their form, and it is possible that they actively seize oil-droplets and other minute solid food particles. The cell passes the fat to its deeper end and, thence, out into the subjacent lymphoid tissue. It is probable that here certain amœboid cells of the adenoid tissue pick it up, and carry it into the central lacteal of a villus, where they break up and set it free. In the villus there are all the anatomical arrangements for a mechanism which shall actively suck substances into it. Each is more or less

elastic, and moreover, its capillary network when filled with blood will distend it. If its plain muscular layer contracts and compresses it, causing its central lacteal to empty into vessels lying deeper in the intestinal wall, the villus will actively expand again so soon as its muscles relax. In so doing it cannot fill its lacteals from the deeper vessels on account of the valves in the latter, and, accordingly, must tend to draw into itself materials from the intestines; much like a sponge re-expanding in water, after having been squeezed dry. The liquid thus sucked up may draw oil-drops with it, into the free ends of the cells and between them; and by repetitions of the process it is possible that considerable quantities of liquid, with suspended oil-drops, might be carried into the epithelial cells covering a villus. The bile moistening the surface of the villus may facilitate the passage of oil, and it is also said to stimulate the contractions of the villi; if so, its efficacy in promoting the absorption of fats will be explained, in spite of its chemical inertness with respect to those bodies. There is also reason to believe that a good deal of the emulsified fat is also directly picked up by amœboid corpuscles, which push their way between the epithelial cells and thrusting processes into the intestine, pick up oil-droplets, and then travel back and convey their load to the lacteal.

The path taken by peptones is uncertain. They seem to be very rapidly converted into proteids (? serum albumin) after absorption as they cannot be found, or only traces of them, in the thoracic duct or the portal vein blood of a digesting animal. Moreover, peptones directly injected into the blood are poisonous. Probably they are seized upon and transformed by the cells of the lymphoid tissue.

Digestion in the Large Intestine. The contractions of the small intestine drive on its continually diminishing contents until they reach the ileo-colic valve, through which they are ultimately pressed. As a rule, when the mass enters the large intestine its nutritive portions have been almost entirely absorbed, and it consists merely of some water, with the indigestible portion of the food and of the secretions of the alimentary canal. It contains cellulose, elastic tissue, mucin, and somewhat-altered bile pigments; some fat if a large quantity has been eaten; and some starch, if raw vegetables have formed part of the diet. In its progress through

the large intestine it loses more water, and the digestion of starch and the absorption of fats is continued. Finally the residue, with some excretory matters added to it in the large intestine, collects in the sigmoid flexure of the colon and in the rectum, and is sent out of the Body from the latter.

The Digestion of an Ordinary Meal. We may best sum up the facts stated in this chapter by considering the digestion of a common meal; say a breakfast consisting of bread and butter, beefsteak, potatoes and milk. Many of these substances contain several alimentary principles, and, since these are digested in different ways and in different parts of the alimentary tract, the first thing to be done is to consider what are the proximate constituents of each. We thus separate the materials of the breakfast as in table on next page.

From such a meal we may first separate the elastin, cellulose, and calcium sulphate, as indigestible and passed out of the Body in the same state and in the same quantity as they entered it. Then come the salines which need no special digestion, and, taken either in solution or dissolved in the saliva or gastric juice, are absorbed from the mouth, stomach, and intestines without further change. Cane and grape sugars experience the same lot, except that any cane sugar or maltose reaching the intestines before absorption is changed into grape sugar by the *succus entericus.* Calcium phosphate will be dissolved by the free acid in the stomach, yielding calcium chloride, which will be absorbed there or in the intestine. Starch will be partially converted into maltose during mastication and deglutition, and it is possible that some of this sugar may be absorbed from the stomach. A great part of the starch will, however, be passed on into the intestine unchanged, since the action of saliva is suspended in the stomach; and its conversion will be completed by the pancreatic secretion, and perhaps by the ptyalin, though this is probably destroyed in the stomach by the gastric juice; but in any case the starch will only have been changed to maltose, and will need further digestive treatment. The various proteids will be partially dissolved in the stomach and converted into peptone, which will in part be absorbed there; the residue, with the undigested proteids, will be passed on to the intestines. There the bile will precipitate the peptones and parapeptones and, with the pancreatic secretion, render the chyme alkaline, and so stop the activity

TABLE SHOWING THE ALIMENTARY PRINCIPLES EATEN AT AN ORDINARY MEAL.

Bread contains....	Water.	Common salt and others.	Calcium phosphate, Calcium sulphate.	Starch.	Grape sugar.	Cellulose.	Small quantities of several	Gluten, Vegetable casein.
Butter contains...	Water.	Common salt and others.	....	....	....			
Cooked Beefsteak contains........	Water.	Potassium phosphate, Common salt and others.	....	....	Grape sugar.			
Potatoes contain...	Water.	....	....	Starch.	....			
Milk contains,....	Water.	Common salt and others, especially phosphates.	Calcium phosphate, Iron phosphate.	....	Milk sugar.			

of the gastric pepsin. The pancreatic secretion will, however, redissolve the precipitated peptone, and the unchanged proteids and parapeptone and the albumose, and turn the three last into peptone, breaking up part of this into leucin and tyrosin; these will be absorbed as they pass along the small intestine; a small quantity perhaps passing into the large intestine, to be taken up there. The fats will remain unchanged until they enter the small intestine, except that the proteid cell-walls of the adipose tissue of the beefsteak will be dissolved away. In the small intestine some of these little oil masses will be in part saponified, but most will be emulsified and taken up into the lacteals in that condition. Gelatin, from the white fibrous tissue of the beefsteak, will undergo changes in the stomach and intestine, and be dissolved and absorbed.

The substances leaving the alimentary canal after such a meal would be, primarily, the indigestible cellulose and elastin, and some water. But there might also be some unabsorbed fats, starch, and salts. To these would be added, in the alimentary canal, mucin, some of the ferments of the digestive secretions, some slightly altered bile pigments, and other bodies excreted by the large intestine.

Dyspepsia is the common name of a number of diseased conditions attended with loss of appetite or troublesome digestion. Being often unattended with acute pain, and if it kills at all doing so very slowly, it is pre-eminently suited for treatment by domestic quackery. In reality, however, the immediate cause of the symptoms, and the treatment called for, may vary widely; and their detection and the choice of the proper remedial agents often call for more than ordinary medical skill. A few of the more common forms of dyspepsia may be mentioned here, with their proximate causes, not in order to enable people to undertake the rash experiment of dosing themselves, but to show how wide a chance there is for any unskilled treatment to miss its end, and do more harm than good.

Appetite is primarily due to a condition of the mucous membrane of the stomach which, in health, comes on after a short fast, and stimulates its sensory nerves; and loss of appetite may be due to either of several causes. The stomach may be apathetic and lack its normal sensibility, so that the empty condition does not act, as it normally does, as a suffi-

cient excitant. When food is taken it is a further stimulus and may be enough; in such cases "appetite comes with eating." A bitter before a meal is useful as an appetizer to patients of this sort. On the other hand, the stomach may be too sensitive, and a voracious appetite be felt before a meal, which is replaced by nausea, or even vomiting, as soon as a few mouthfuls have been swallowed; the extra stimulus of the food then overstimulates the too irritable stomach, just as a draught of mustard and warm water will a healthy one. The proper treatment in such cases is a soothing one. When food is taken it ought to stimulate the sensory gastric nerves, so as to excite the reflex centres for the secretory nerves, and for the dilatation of the blood-vessels of the organ; if it does not, the gastric juice will be imperfectly secreted. In such cases one may stimulate the secretory nerves by weak alkalies, as certain mineral waters or a little carbonate of soda, before meals; or give drugs, as strychnine, which increase the irritability of reflex nerve-centres. The vascular dilatation may be helped by warm drinks, and this is probably the *rationale* of the glass of hot water after eating which has often been found useful; the usual small cup of hot coffee after dinner is a more agreeable form of the same aid to digestion. In states of general debility, when the stomach is too feeble to secrete under any stimulation, the administration of weak acids and artificially prepared pepsin is needed, to supply gastric juice from outside, until the improved digestion strengthens the stomach up to the point of being able to do its own work.

Enough has probably been said to show that dyspepsia is not a disease, but a symptom accompanying many pathological conditions, requiring special knowledge for their treatment. From its nature—depriving the Body of its proper nourishment—it tends to intensify itself, and so should never be neglected; a stitch in time saves nine.

The Movements of the Intestines. When the abdomen of a living anæsthetized animal is opened, especially during digestion, contractions are seen slowly travelling along the bowels, which have in consequence somewhat the appearance of a writhing mass of worms, hence the name *vermicular* often given to these movements: they are also called *peristaltic.* On observing a portion of the gut a narrowing due to contraction of its circular muscular coat will be seen to

pass slowly along it, normally in a direction towards the rectum; these contractions push before them part of the contents of the intestine. The simultaneous contractions of the outer longitudinal layer of the muscular coat are not so marked or so easily directly observable. If the bowels be entirely removed from the body of the animal the movements go on for some time, so they are obviously not directly dependent on extrinsic nerves. They are probably primarily due to a slight automaticity of the muscle itself, which as in the case of the heart (Chap. XVII) is favored by distension, but they may be due to nerve impulses arising in the cells of the plexus of Auerbach. As in the case of the heart these movements are under control of extrinsic nerve-fibres, originating in the cerebro-spinal centre, and these fibres are excitor and depressor. Exactly contrary to that which we find in the case of the heart, the fibres reaching the intestines through the pneumogastrics are excitor, causing more powerful contractions, and the fibres coming from the sympathetic through the splanchnics (where they are mixed with but quite distinct from the vaso-constrictor fibres) are inhibitory. Stimulation of the splanchnic nerves will bring actively contracting intestines to rest. The influence of the central nervous system on the motions of the bowel is shown by the contractions caused by fright or other strong emotions, illustrated by the Hebrew phrase "bowels moved with compassion." Deficiency of arterial blood excites powerful intestinal contractions. The various purgative medicines act in very different ways; some directly on the intestinal neuro-muscular apparatus; some on the extrinsic nerve centres concerned; some (as Epsom salts) mainly by causing a great secretion of liquid into the bowel and so distending it.

CHAPTER XXV.

THE RESPIRATORY MECHANISM.

Definitions. The blood as it flows from the right ventricle of the heart, through the lungs, to the left auricle, loses carbon dioxide and gains oxygen. In the systemic circulation exactly the reverse changes take place, oxygen leaving the blood to supply the living tissues; and carbon dioxide, generated in them, passing back into the blood capillaries. The oxygen loss and carbon dioxide gain are associated with a change in the color of the blood from bright scarlet to purple red, or from arterial to venous; and the opposite changes in the lungs restore to the dark blood its bright tint. The whole set of processes through which blood becomes venous in the systemic circulation and arterial in the pulmonary—in other words the processes concerned in the gaseous reception, distribution and elimination of the Body—constitute the function of *respiration;* so much of this as is concerned in the interchanges between the blood and air being known as *external respiration;* while the interchanges occurring in the systemic capillaries, and the processes in general by which oxygen is fixed and carbon dioxide formed by the living tissues, are known as *internal respiration.* When the term respiration is used alone, without any limiting adjective, the external respiration only, is commonly meant.

Respiratory Organs. The blood being kept poor in oxygen and rich in carbon dioxide by the action of the living tissues, a certain amount of gaseous interchange will nearly always take place when it comes into close proximity to the surrounding medium; whether this be the atmosphere itself or water containing air in solution. When an animal is small there are often no special organs for its external respiration, its general surface being sufficient (especially in aquatic animals with a moist skin) to permit of all the gaseous exchange that is necessary. In the simplest creatures, indeed, there is even no blood, the cell or cells composing

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them taking up for themselves from their environment the oxygen which they need, and passing out into it their carbon dioxide waste; in other words, there is no differentiation of the external and internal respirations. When, however, an animal is larger many of its cells are so far from a free surface that they cannot transact this give-and-take with the surrounding medium directly, and the blood, or some liquid representing it in this respect, serves as a middleman between the living tissues and the external oxygen; and then one usually finds special *respiratory organs* developed, to which the blood is brought to make good its oxygen loss and get rid of its excess of carbon dioxide. In aquatic animals such organs take commonly the form of gills; these are protrusions of the body over which a constant current of water, containing oxygen in solution, is kept up; and in which blood capillaries form a close network immediately beneath the surface. In air-breathing animals a different arrangement is usually found. In some, as frogs, it is true, the skin is always moist and serves as an important respiratory organ, large quantities of venous blood being sent to it for aëration. But for the occurrence of the necessary gaseous diffusion, the skin must be kept very moist, and this, in a terrestrial animal, necessitates a great amount of secretion by the cutaneous glands to compensate for evaporation; accordingly in most land animals the air is carried into the body through tubes with narrow external orifices and so the drying up of the breathing surfaces is greatly diminished; just as water in a bottle with a narrow neck will evaporate much more slowly than the same amount exposed in an open dish. In insects (as bees, butterflies, and beetles) the air is carried by tubes which split up into extremely fine branches and ramify all through the body, even down to the individual tissue elements, which thus carry on their gaseous exchanges without the intervention of blood. But in the great majority of air-breathing animals the arrangement is different; the air-tubes leading from the exterior of the body do not subdivide into branches which ramify all through it, but open into one or more large sacs to which the venous blood is brought, and in whose walls it flows through a close capillary network. Such respiratory sacs are called *lungs*, and it is a highly developed form of them which is employed in the Human Body.

The Air-Passages and Lungs. In our own Bodies some

small amount of respiration is carried on in the alimentary canal, the air swallowed with food or saliva undergoing gaseous exchanges with the blood in the gastric and intestinal mucous membranes. The amount of oxygen thus obtained by the blood is however very trivial, as is that absorbed through the skin, covered as it is by its dry horny non-vascular epidermis. All the really essential gaseous interchanges between the Body and the atmosphere take place in the lungs, two large sacs (*lu*, Fig. 1) lying in the thoracic cavity, one on each side of the heart. To these sacs the air is conveyed through a series of passages. Entering the pharynx through the nostrils or mouth, it passes out of this by the opening leading into the larynx, or voice-box (*a*, Fig. 122), lying in

Fig. 122.—The lungs and air-passages seen from the front. On the left of the figure the pulmonary tissue has been dissected away to show the ramifications of the bronchial tubes. *a*, larynx; *b*, trachea; *d*, right bronchus. The left bronchus is seen entering the *root* of its lung.

the upper part of the neck (the communication of the two is seen in Fig. 107); from the larynx passes back the *trachea* or windpipe, *b*, which, after entering the chest cavity, divides into the *right* and *left bronchi, d, e.* Each bronchus divides up into smaller and smaller branches, called *bronchial tubes*, within the lung on its own side; and the smallest bronchial tubes end in sacculated dilatations, the *infundibula* of the lungs, the sacculations (Fig. 124) being the *alveoli:* the word "cell" being here used in its primitive sense of a small cavity, and not in its later technical signification of a morphological unit of the Body. On the walls of the air-cells the pulmonary capillaries ramify, and it is in them that the interchanges of the external respiration take place.

Fig. 123.—A small bronchial tube, *a*, dividing into its terminal branches, *c*; these have pouched or sacculated walls and end in the sacculated infundibula, *b*.

Structure of the Trachea and Bronchi. The windpipe may readily be felt in the middle line of the neck, a little below

Adam's apple, as a rigid cylindrical mass. It consists fundamentally of a fibrous tube in which cartilages are imbedded, so as to keep it from collapsing; and is lined internally by a mucous membrane covered by several layers of epithelium cells, of which the superficial is ciliated. The elastic cartilages imbedded in its walls are imperfect rings, each somewhat the shape of a horse shoe, and the deficient part of each ring being turned backwards, it comes to pass that the deeper or dorsal side of the windpipe has no hard parts in it. Against this side the gullet lies, and the absence there of the cartilages no doubt facilitates swallowing. The bronchi resemble the windpipe in structure.

The Structure of the Lungs. These consist of the bronchial tubes and their terminal dilatations; numerous bloodvessels, nerves and lymphatics; and an abundance of connective tissue, rich in elastic fibres, binding all together. The bronchial tubes ramify in a tree-like manner (Fig. 122). In structure the larger ones resemble the trachea, except that the cartilage rings are not regularly arranged so as to have their open parts all turned one way. As the tubes become smaller their constituents thin away; the cartilages become less frequent and finally disappear; the epithelium is reduced to a single layer of cells which, though still ciliated, are much shorter than the columnar superficial cell-layer of the larger tubes. The terminal alveoli (*a, a,* Fig. 124), and the air-cells, *b,* which open into them, have walls composed mainly of elastic tissue and lined by a single layer of flat, non-ciliated epithelium, immediately beneath which is a very close network of capillary blood-vessels. The air entering by the bronchial tube is thus only separated from the blood by the thin capillary wall and the thin epithelium, both of which are moist, and well adapted to permit gaseous diffusion.

FIG. 124.—Two infundibula of the lung much magnified *b, b,* the air-cells, or hollow protrusions of the alveolus, opening into its central cavity; *c,* terminal branches of a bronchial tube

The Pleura. Each lung is covered, except at one point, by an elastic serous membrane which adheres tightly to it and

is called the *pleura ;* that point at which the pleura is wanting is called the *root* of the lung and is on its median side; it is there that its bronchus, blood-vessels and nerves enter it. At the root of the lung the pleura turns back and lines the inside of the chest cavity, as represented by the dotted line in the diagram Fig. 3. The part of the pleura attached to each lung is its *visceral,* and that attached to the chest-wall its *parietal layer.* Each pleura thus forms a closed sac surrounding a *pleural cavity,* in which, during health, there are found a few drops of lymph, keeping its surfaces moist. This lessens friction between the two layers during the movements of the chest-walls and the lungs; for although, to insure distinctness, the visceral and parietal layers of the pleura are represented in the diagram as not in contact, that is not the natural condition of things; the lungs are in life distended so that the visceral pleura rubs against the parietal, and the pleural cavity is practically obliterated. This is due to the pressure of the atmosphere exerted through the air-passages on the interior of the lungs. The lungs are extremely elastic and distensible, and when the chest cavity is perforated each shrivels up just as an indian-rubber bladder does when its neck is opened; the reason being that then the air presses on the outside of each with as much force as it does on the inside. These two pressures neutralizing one another, there is nothing to overcome the tendency of the lungs to collapse. So long as the chest-walls are whole, however, the lungs remain distended. The pleural sac is air-tight and contains no air, and the pressure of the air around the Body is borne by the rigid walls of the chest and prevented from reaching the lungs; consequently no atmospheric pressure is exerted on their outside. On their interior, however,
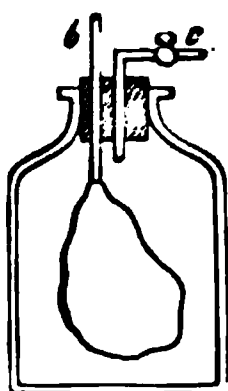
the atmosphere presses with its full weight, equal to about 90 centigrams on a square centimeter (14.5 lbs. on the square inch), and this is far more than sufficient to distend the lungs so as to make them completely fill all the parts of the thoracic cavity not occupied by other organs. Suppose *A* (Fig. 125) to be a bottle closed air-tight by a cork through which two tubes pass, one of which, *b,* leads into an elastic bag, *d,* and the other, *c,* provided with a stop-cock, opens freely

below into the bottle. When the stop-cock, *c,* is open the air will enter the bottle and press there on the outside of the bag, as well as on its inside through *b.* The bag will therefore collapse, as the lungs do when the chest cavity is opened. But if some air be sucked out through *c* the pressure of that remaining in the bottle will diminish, and of that inside the bag will be unchanged, and the bag will thus be blown up, because the atmospheric pressure on its interior will not be balanced by that on its exterior. At last, when all the air is sucked out of the bottle and the stop-cock on *c* closed, the bag, if sufficiently distensible, will be expanded so as to completely fill the bottle and press against its inside, and the state of things will then answer to that naturally found in the chest. If the bottle were now increased in size without letting air into it, the bag would expand still more, so as to fill it, and in so doing would receive air from outside through *b;* and if the bottle then returned to its original size, its walls would press on the bag and cause it to shrink and expel some of its air through *b.* Exactly the same must of course happen, under similar circumstances, in the chest, the windpipe answering to the tube *b* through which air enters or leaves the elastic sac.

The Respiratory Movements. The air taken into the lungs soon becomes laden in them with carbon dioxide, and at the same time loses much of its oxygen; these interchanges take place mainly in the deep recesses of the alveoli, far from the exterior and only communicating with it through a long tract of narrow tubes. The alveolar air, thus become unfit to any longer convert venous blood into arterial, could only very slowly be renewed by gaseous diffusion with the atmosphere through the long air-passages—not nearly fast enough for the requirements of the Body, as one learns by the sensation of suffocation which follows holding the breath for a short time with mouth and larynx open. Consequently co-operating with the lungs is a *respiratory mechanism,* by which the air within them is periodically mixed with fresh air taken from the outside, and also the air in the alveoli is stirred up so as to bring fresh layers of it in contact with the walls of the air-cells. This mixing is brought about by the breathing movements, consisting of regularly alternating *in-spirations,* during which the chest cavity is enlarged and fresh air enters the lungs, and *expirations,* in which the cav-

ity is diminished and air expelled from the lungs. When the chest is enlarged the air the lungs contain immediately distends them so as to fill the larger space; in so doing it becomes rarefied and less dense than the external air; and since gases flow from points of greater to those of less pressure, some outside air at once flows in by the air-passages and enters the lungs. In expiration the reverse takes place. The chest cavity, diminishing, presses on the lungs and makes the air inside them denser than the external air, and so some passes out until an equilibrium of pressure is restored. The chest, in fact, acts very much like a bellows. When the bellows are opened air enters in consequence of the rarefaction of that in the interior, which is expanding to fill the larger space; and when the bellows are closed again it is expelled. To make the bellows quite like the lungs we must, however, as in Fig. 126, have only one opening in them, that of the nozzle, for both the entry and exit of the air; and this opening should lead, not directly into the bellows cavity, but into an elastic bag lying in it, and tied to the inner end of the nozzle-pipe. This sac would represent the lungs and the space between its outside and the inside of the bellows, the pleural cavities.

Fig. 126.—Diagram to illustrate the entry of air to the lungs when the thoracic cavity enlarges.

We have next to see how the expansion and contraction of the chest cavity are brought about.

The Structure of the Thorax. The thoracic cavity has a conical form determined by the shape of its skeleton (Fig. 127), its narrower end being turned upwards. Dorsally, ventrally, and on the sides, it is supported by the rigid framework afforded by the thoracic vertebræ, the breast-bone, and the ribs. Between and over these lie muscles, and the whole is covered in, air-tight, by the skin externally, and the parietal layers of the pleuræ inside. Above, its aperture is closed by muscles and by various organs passing between the thorax and the neck; and below it is bounded by the *diaphragm*, which forms a movable bottom to the, otherwise, tolerably rigid box. In inspiration this box is increased in all its diameters—dorso-ventrally, laterally, and from above down.

The Vertical Enlargement of the Thorax. This is brought about by the contraction of the diaphragm which (Figs. 1 and 128) is a thin muscular sheet, with a fibrous membrane, serving as a tendon, in its centre. In rest, the diaphragm is dome-shaped, its concavity being turned towards the abdomen. From the tendon on the crown of the dome striped muscular fibres radiate, downwards and outwards, to all sides; and are fixed by their inferior ends to the lower ribs, the breast-bone, and the vertebral column. In expiration the lower lateral portions of the diaphragm lie close against the chest-walls, no lung intervening between them. In inspiration the muscular fibres, shortening, flatten the dome

Fig. 127.—The skeleton of the thorax. *a, g,* vertebral column; *b,* first rib: *c,* clavicle; *d.* bird rib; *f,* glenoid fossa.

and enlarge the thoracic cavity at the expense of the abdominal; and at the same time its lateral portions are pulled away from the chest-walls, leaving a space into which the lower ends of the lungs expand. The contraction of the diaphragm thus increases greatly the size of the thorax chamber by adding to its lowest and widest part.

The Dorso-Ventral Enlargement of the Thorax. The ribs on the whole slope downwards from the vertebral column to the breast-bone, the slope being most marked in the lower ones. During inspiration the breast-bone

and the sternal ends of the ribs attached to it are raised,
and so the distance between the sternum and the vertebral

1

column is increased. That this must be so will readily be
seen on considering the diagram Fig. 129, where *ab* repre-
sents the vertebral column, *c* and *d* two
ribs, and *st* the sternum. The continu-
ous lines represent the natural position
of the ribs at rest in expiration, and the
dotted lines the position in inspiration.
It is clear that when their lower ends
are raised, so as to make the bars lie in
a more horizontal plane, the sternum is
pushed away from the spine, and so the
chest cavity is increased dorso-ventrally.
The inspiratory elevation of the ribs is
mainly due to the action of the *scalene*
and *external intercostal muscles.* The
scalene muscles, three on each side, arise

FIG. 129.—Diagram illus-
trating the dorso ventral
increase in the diameter of
the thorax when the ribs
are raised.

from the cervical vertebræ, and are inserted into the upper
ribs. The external intercostals (Fig. 113, *A*) lie between the
ribs and extend from the vertebral column to the costal carti-
lages; their fibres slope downwards and forwards. During
an inspiration the scalenes contract and fix the upper ribs
firmly; then the external intercostals shorten and each raises
the rib below it. The muscle, in fact, tends to pull together
the pair of ribs between which it lies, but as the upper one of
these is held tight by the scalenes and other muscles above,

the result is that the lower rib is pulled up, and not the upper down.   In this way the lower ribs are raised much more than the upper, for the whole external intercostal muscles on each side may be regarded as one great muscle with many bellies, each belly separated from the next by a tendon, represented by the rib.   When the whole muscular sheet is fixed above and contracts, it is clear that its lower end will be raised more than any intermediate point, since there is a greater length of contracting muscle above it.   The elevation of the ribs tends to diminish the vertical diameter of the chest; this is

Fig. 130.—Portions of four ribs of a dog with the muscles between them. *a, a,* ventral ends of the ribs, joining at *c* the rib cartilages, *b,* which are fixed to cartilaginous portions, *d,* of the sternum. *A,* external intercostal muscle, ceasing between the rib cartilages, where the internal intercostal, *B,* is seen. Between the middle two ribs the external intercostal muscle has been dissected away, so as to display the internal which was covered by it.

more than compensated for by the simultaneous descent of the diaphragm.

The Lateral Enlargement of the Chest is mainly due to the diaphragm, which, when it contracts, adds to the lowest and widest part of the conical chest cavity. Some small widening is, however, brought about by a rotation of some of the middle ribs which, as they are raised, roll round a little at their vertebral articulations and twist their cartilages. Each rib is curved and, if the bones be examined in their natural position in a skeleton, it will be seen that the most

curved part lies below the level of a straight line drawn from the vertebral to the sternal attachment of the bone. By the rotation of the rib, during inspiration, this curved part is raised and turned out, and the chest widened. The mechanism can be understood by clasping the hands opposite the lower end of the sternum and a few inches in front of it, with the elbows bent and pointing downwards. Each arm will then answer, in an exaggerated way, to a curved rib, and the clasped hands to the breast-bone. If the hands be simply raised a few inches by movement at the shoulder-joints only, they will be separated farther from the front of the Body, and rib elevation and the consequent dorso-ventral enlargement of the cavity surrounded will be represented. But if, simultaneously, the arms be rotated at the shoulder-joints so as to raise the elbows and turn them out a little, it will be seen that the space surrounded by the two arms is considerably increased from side to side, as the chest cavity is in inspiration by the similar elevation of the most curved part or "angle" of the middle ribs.

Expiration. To produce an inspiration requires considerable muscular effort. The ribs and sternum have to be raised; the elastic rib cartilages bent and somewhat twisted; the abdominal viscera pushed down; and the abdominal wall pushed out to make room for them. In expiration, on the contrary, but little, if any, muscular effort is needed. As soon as the muscles which have raised the ribs and sternum relax, these tend to return to their natural unconstrained position, and the rib cartilages, also, to untwist themselves and bring the ribs back to their position of rest; the elastic abdominal wall presses the contained viscera against the under side of the diaphragm, and pushes that up again as soon as its muscular fibres cease contracting. By these means the chest cavity is restored to its original capacity and the air sent out of the lungs, rather by the elasticity of the parts which were stretched or twisted in inspiration, than by any special expiratory muscles.

Forced Respiration. When a very deep breath is drawn or expelled, or when there is some impediment to the entry or exit of the air, a great many muscles take part in producing the respiratory movements; and expiration then becomes, in part, an actively muscular act. The main expiratory muscles are the *internal intercostals* which lie beneath the exter-

nal between each pair of ribs (Fig. 130 *B*), and have an oppo-
site direction, their fibres running upwards and forwards. In
forced expiration the lower ribs are fixed or pulled down by
muscles running in the abdominal wall from the pelvis to
them and to the breast-bone. The internal intercostals, con-
tracting, pull down the upper ribs and the sternum, and so
diminish the thoracic cavity dorso-ventrally. At the same
time, the contracted abdominal muscles press the walls of
that cavity against the viscera within it, and pushing these
up forcibly against the diaphragm make it very convex
towards the chest, and so diminish the latter in its vertical
diameter. In very violent expiration many other muscles
may co-operate, tending to fix points on which those muscles
which can directly diminish the thoracic cavity, pull. In
violent inspiration, also, many extra muscles are called into
play. The neck is held rigid to give the scalenes a firm at-
tachment; the shoulder-joint is held fixed and muscles going
from it to the chest-wall, and commonly serving to move the
arm, are then used to elevate the ribs; the head is held firm
on the vertebral column by the muscles going between the
two, and then other muscles, which pass from the collar-bone
and sternum to the skull, are used to pull up the former.
The muscles which are thus called into play in labored but
not in quiet breathing are called *extraordinary muscles of
respiration.*

The Respiratory Sounds. The entry and exit of air
are accompanied by *respiratory sounds* or *murmurs,* which
can be heard on applying the ear to the chest wall. The
character of these sounds is different and characteristic over
the trachea, the larger bronchial tubes, and portions of lung
from which large bronchial tubes are absent. They are vari-
ously modified in pulmonary affections, and hence the value
of *auscultation* of the lungs in assisting the physician to
form a diagnosis.

The Capacity of the Lungs. Since the chest cavity
never even approximately collapses, the lungs are never com-
pletely emptied of air: the space they have to occupy is
larger in inspiration than during expiration, but is always
considerable, so that after a forced expiration they still con-
tain a large amount of air which can only be expelled from
them by opening the pleural cavities; then they entirely col-
lapse, just as the bag in Fig. 125 would if the bottle inclosing

it were broken. The capacity of the chest, and therefore of the lungs, varies much in different individuals, but in a man of medium height there remain in the lungs after the most violent possible expiration, about 1640 cub. cent. (100 cub. inches) of air, called the *residual air.* After an ordinary expiration there will be in addition to this about as much more *supplemental air ;* the residual and supplemental together forming the *stationary air,* which remains in the chest during quiet breathing. In an ordinary inspiration 500 cub. cent. (30 cub. inches) of *tidal air* are taken in, and about the same amount is expelled in natural expiration. By a forced inspiration about 1600 cub. cent. (98 cub. inches) of *complemental air* can be added to the tidal air. After a forced inspiration therefore the chest will contain 1640 + 1640 + 500 + 1600 = 5380 cubic centimeters (328 cubic inches) of air. The amount which can be taken in by the most violent possible inspiration after the strongest possible expiration, that is, the supplemental, tidal, and complemental air together, is known as the *vital capacity.* For a healthy man 1.7 meters (5 feet 8 inches) high it is about 3700 cub. cent. (225 cub. inches) and increases 60 cub. cent. for each additional centimeter of stature; or about 9 cubic inches for each inch of height.

The Quantity of Air Breathed Daily. Knowing the quantity of air taken in at each breath and expelled again (after more or less thorough admixture with the stationary air) we have only to know, in addition, the rate at which the breathing movements occur, to be able to calculate how much air passes through the lungs in twenty-four hours. The average number of respirations in a minute is found by counting on persons sitting quietly, and not knowing that their breathing rate is under observation, to be fifteen in a minute. In each respiration half a liter (30 cubic inches) of air is concerned; therefore 0.5 × 15 × 60 × 24 = 10,800 liters (375 cubic feet) is the quantity of air breathed under ordinary circumstances by each person in a day.

Hygienic Remarks. Since the diaphragm when it contracts pushes down the abdominal viscera beneath it, these have to make room for themselves by pushing out the soft front of the abdomen which, accordingly, protrudes when the diaphragm descends. Hence breathing by the diaphragm, being indicated on the exterior by movements of the abdo-

men, is often called "abdominal respiration," as distinguished from breathing by the ribs, called "costal" or "chest breathing." In both sexes the diaphragmatic breathing is the most important, but, as a rule, men and children use the ribs less than adult women. Since both abdomen and chest alternately expand and contract in healthy breathing, anything which impedes their free movement is to be avoided; and the tight lacing which used to be thought elegant a few years back, and is still indulged in by some who think a distorted form beautiful, seriously impedes one of the most important functions of the Body, leading, if nothing worse, to shortness of breath and an incapacity for muscular exertion. In extreme cases of tight lacing some organs are often directly injured, weals of fibrous tissue being, for example, not unfrequently found developed on the liver, from the pressure of the lower ribs forced against it by a tight corset.

The Aspiration of the Thorax. As already pointed out, the external air cannot press directly upon the contents of the thoracic cavity, on account of the rigid framework which supports its walls; it still, however, presses on them indirectly through the lungs. Pushing on the interior of these with a pressure equal to that exerted on the same area by a column of mercury 760 mm. (30 inches) high, it distends them and forces them against the inside of the chest-walls, the heart, the great thoracic blood-vessels, the thoracic-duct, and the other contents of the chest-cavity. This pressure is not equal to that of the external air, since some of the total air-pressure on the inside of the lungs is used up in overcoming their elasticity, and it is only the residue which pushes them against the things outside them. In expiration this residue is equal to that exerted by a column of mercury 754 mm. (29.8 inches) high. On most parts of the Body the atmospheric pressure acts, however, with full force. Pressing on a limb it pushes the skin against the soft parts beneath, and these compress the blood and lymph vessels among them; and the yielding abdominal walls do not, like the rigid thoracic walls, carry the atmospheric pressure themselves, but transmit it to the contents of the cavity. It thus comes to pass that the blood and lymph in most parts of the Body are under a higher atmospheric pressure than they are exposed to in the chest, and consequently these liquids tend to flow into the thorax, until the extra distention of the vessels in

which they there accumulate compensates for the less external pressure to which those vessels are exposed. An equilibrium would thus very soon be brought about were it not for the respiratory movements, in consequence of which the intra-thoracic pressure is alternately increased and diminished, and the thorax comes to act as a sort of suction-pump on the contents of the vessels of the Body outside it; thus the respiratory movements influence the circulation of the blood and the flow of the lymph.

Influence of the Respiratory Movements upon the Circulation. Suppose the chest in a condition of normal expiration and the external pressure on the blood in the blood-vessels within it and in the heart, to have come, in the manner pointed out in the last paragraph, into equilibrium with the atmospheric pressure exerted on the blood-vessels of the neck and abdomen. If an inspiration now occurs, the chest cavity being enlarged the pressure on all of its contents will be diminished. In consequence, air enters the lungs from the windpipe, and blood enters the venæ cavæ and the right auricle of the heart. Thus not only the lungs, but the right side of the heart, and the intra-thoracic portions of the systemic veins leading to it, are expanded during an inspiration; but the lungs being much the most distensible take far the greatest part in filling up the increased space. The left side of the heart is not much influenced as it is filled from the pulmonary veins; and the whole vessels of the lesser circulation lying within the chest, and being all affected in the same way at the same time, the blood-flow in them is not directly influenced by the aspiration of the thorax. Distention of the lungs seems, however, to diminish the capacity of their vessels, and so to a certain extent the flow is influenced; as the lungs expand blood is forced out of their vessels into the left auricle, and when they again contract their vessels fill up from the right ventricle. The pressure on the thoracic aorta being diminished in inspiration, blood tends to flow back into it from the abdominal portion of the vessel, but cannot enter the heart on account of the semilunar valves; and the back-flow does not in any case equal the onflow due to the beat of the heart; so what happens in the aorta is but a slight slowing of the current. The general result of all this is that the circulation is considerably assisted. When the next expiration occurs, and the pressure in the thorax again

rises, air and blood both tend to be expelled from the cavity. The aorta thus regains what it lost during inspiration; the pressure on it is increased and it empties itself faster into its abdominal portion. The semilunar valves having prevented any regurgitation into the heart, there is neither gain nor loss so far as it is concerned. With the systemic intra-thoracic veins, however, this is not the case; the extra blood entering them has already in great part gone on beyond the tricuspid valve, and cannot flow back during expiration; and the pressure in the auricle being constantly kept low by its emptying into the ventricle, the increased pressure on the venæ cavæ tends rather to send blood on into the heart, than back into the extra-thoracic veins. Moreover, whatever blood tends to take the latter course cannot do it effectually since, although the venæ cavæ themselves contain no valves, the more distant veins which open into them do. Consequently, whatever extra blood has, to use the common phrase, been "sucked" into the intra-thoracic venæ cavæ in inspiration and has not been sent already on into the right ventricle before expiration occurs, is, on account of the venous valves, imprisoned in the cavæ under an increased pressure during expiration; and this tends to make it flow faster into the auricle during the diastole of the latter. How much the alternating respiratory movements assist the venous flow is shown by the dilation of the veins of the head and neck which occurs when a person is holding his breath; and the blackness for the face, from distention of the veins and stagnation of the capillary flow, which occurs during a prolonged fit of coughing, which is a series of expiratory efforts without any inspirations.

On the whole the influence of the respiratory movements on the blood-flow is such as to favor it in inspiration and to impede it during expiration. This influence very often shows itself on tracings of arterial pressure taken as described in Chap. XVIII. Such tracings usually show in addition to the pulse waves, slower and greater rises and falls of pressure which have the same rhythm as the respiration. In general, the rise of pressure in these *respiratory waves* of blood-pressure is synchronous with inspiration and the fall with expiration, but not exactly. The changes manifest themselves on the blood-pressure curve a little later than the commencement of the thoracic movement which leads to them; the rise be-

ginning a little after the beginning of inspiration, the fall a little later than the commencement of expiration.

In still another way the aspiration of the thorax assists the heart. The heart and lungs are both distensible, though in different degrees, and each is stretched in the chest somewhat beyond its natural size; the one by the atmospheric pressure directly, the other by that pressure indirectly exerted through the blood exposed to it in the extra-thoracic veins. Supposing, therefore, the heart suddenly to shrink, it would leave more space in the chest to be filled by the lungs; these must accordingly, at each cardiac systole, expand a little to fill the extra room, just as they do when the space around them is otherwise enlarged, as during an inspiration. The elasticity of the lungs, however, causes them to resist this distention and oppose the cardiac systole. The matter may be made clear by an arrangement like that in Fig. 131. *A* is an air-tight vessel with a tube, *e*, provided with a stopcock, leading from it; *b* is a highly distensible elastic bag in free communication through *d* with the exterior; and *c*, representing the heart, is a less extensible sac, from which a tube leads and dips under water in the vessel *B*. If air be pumped out through *e* both bags will dilate, *b* filling with air, and *c* with water driven up by atmospheric pressure. Ultimately, if sufficiently extensible, they would fill the whole space, the thinner-walled, *b*, occupying most of it. If then the stop-cock be closed, things will remain in equilibrium, each bag striving to collapse and so exerting a pull on the other, for if *b* shrinks *c* must expand and *vice versa*.

Fig. 131.—Diagram illustrating the influence of aspiration of the thorax on the circulation of the blood.

If *c* suddenly shrink, as the heart does in its systole, *b* will dilate; but as soon as the systole of *c* ceases, *b* will shrink again and pull *c* out to its previous size. In the same way, after the cardiac systole, when the heart-walls relax, the lungs pull them out again and dilate the organ. The contracting heart thus expends some of its work in overcoming the elasticity of the lungs, which opposes their expansion to fill the space left by the smaller heart; but during the diastole of the heart this work is utilized to pull out its walls again, and

draw blood into it. Since the normal heart has muscular power, and to spare, for its systole, this arrangement, by which some of the work then spent is stored away to assist the diastole, which cannot be directly performed by cardiac muscles, is of service to it on the whole. It is a physiological though not a mechanical advantage; no work power is gained, but what there is, is better distributed.

Influence of the Respiration on the Lymph-Flow. During inspiration, when intra-thoracic pressure is lowered, lymph is pressed into the thoracic duct from the abdominal lymphatics. In expiration, when thoracic pressure rises again, the extra lymph cannot flow back on account of the valves in the lymphatic vessels, and it is consequently driven on to the cervical ending of the thoracic duct. The breathing movements thus pump the lymph on.

CHAPTER XXVI.

THE CHEMISTRY OF RESPIRATION.

Nature of the Problems. The study of the respiratory process from a chemical standpoint has for its object to discover what are, in kind and extent, the interchanges between the air in the lungs and the blood in the pulmonary capillaries; and the nature and amount of the corresponding gaseous changes between the living tissues, and the blood in the systemic capillaries. Neglecting some oxygen used up otherwise than in forming carbon dioxide, and some carbon dioxide eliminated by other organs than the lungs, these processes in the long-run balance, the blood losing as much carbon dioxide gas in the lungs as it gains elsewhere, and gaining as much oxygen in the lungs as it loses in the systemic capillaries. To comprehend the matter it is necessary to know the physical and chemical conditions of these gases in the lungs, in the blood, and in the tissues generally; for only so can we understand how it is that in different localities of the Body such exactly contrary processes occur. So far as the problems connected with the external respiration are concerned our knowledge is tolerably complete; but as regards the internal respiration, taking place all through the Body, much has yet to be learnt; we know that a muscle at work gives more carbon dioxide to the blood than one at rest and takes more oxygen from it, but how much of the one it gives and of the other it takes is only known approximately; as are the conditions under which this greater interchange during the activity of the muscular tissue is effected: and concerning nearly all the other issues we know even less than about muscle. In fact, as regards the Body as a whole, it is comparatively easy to find how great its gaseous interchanges with the air are during work and rest, waking and sleeping,

while fasting or digesting, and so on ; but when it comes to be decided what organs are concerned in each case in producing the greater or less exchange, and how much of the whole is due to each of them, the question is one far more difficult to settle and still very far from completely answered.

The Changes Produced in Air by being once Breathed. These are fourfold—changes in its temperature, in its moisture, in its chemical composition, and its volume.

The air taken into the lungs is nearly always cooler than that expired, which has a temperature of about 36° C. (97° F.). The temperature of a room is usually less than 21° C. (70° F.). The warmer the inspired air the less, of course, the heat which is lost to the Body in the breathing process; its average amount is calculated as about equal to 50 calories in twenty-four hours; a calorie being as much heat as will raise the temperature of one kilogram (2.2 lbs.) of water one degree centigrade (1.8° F.).

The inspired air always contains more or less water vapor, but is rarely saturated; that is, rarely contains so much but it can take up more without showing it as mist; the warmer air is, the more water vapor it requires to saturate it. The expired air is nearly saturated for the temperature at which it leaves the Body, as is readily shown by the water deposited when it is slightly cooled, as when a mirror is breathed upon; or by the clouds seen issuing from the nostrils on a frosty day, these being due to the fact that the air, as soon as it is cooled, cannot hold all the water vapor which it took up when warmed in the Body. Air, therefore, when breathed once, gains water vapor and carries it off from the lungs; the actual amount being subject to variation with the temperature and saturation of the inspired air: the cooler and drier that is, the more water will it gain when breathed. On an average the amount thus carried off in twenty-four hours is about 255 grams (9 ounces). To evaporate this water in the lungs an amount of heat is required, which disappears for this purpose in the Body, to reappear again outside it when the water vapor condenses. The amount of heat taken off in this way during the day is about 148 calories. The total daily loss of heat from the Body through the lungs is therefore 198 calories, 50 in warming the inspired air and 148 in the evaporation of water.

. The most important changes brought about in the

breathed air are those in its chemical composition. Pure air when completely dried consists in each 100 parts of—

	By Volume.	By Weight.
Oxygen	20.8	23
Nitrogen	79.2	77

Ordinary atmospheric air contains in addition 4 volumes of carbon dioxide in 10,000, or 0.04 in 100, a quantity which, for practical purposes, may be neglected. When breathed once, such air gains rather more than 4 volumes in 100 of carbon dioxide, and loses rather more than 5 of oxygen. More accurately, 100 volumes of expired air after drying give 98.9 volumes, which consist of—

Oxygen	15.4
Nitrogen	79.2
Carbon dioxide	4.8

The expired air also contains volatile organic substances in quantities too minute for chemical analysis, but readily detected by the nose upon coming into a close room in which a number of persons have been collected.

Since 10,800 litres (375 cubic feet) of air are breathed in twenty-four hours and lose 5.4 per cent of oxygen, the total quantity of this gas taken up in the lungs daily is 10,800 × 5.4 ÷ 100 = 583.2 litres (20.4 cubic feet). One litre of oxygen measured at 0° C. (32° F.) and under a pressure equal to one atmosphere, weighs 1.43 grams, so the total weight of oxygen taken up by the lungs daily is 583.2 × 1.43 = 833.9 grams. Or, using inches and grains as standards, 44.5 cubic inches of oxygen at the above temperature and pressure weigh almost exactly 16 grains, so the 20.4 cubic feet absorbed in the lungs daily weigh 20.4 × 1728 ÷ 44.5 × 16 = 12,818 grains.

The amount of carbon dioxide excreted from the lungs being 4.3 per cent of the volume of the air breathed daily, is 10,800 × 4.3 ÷ 100 = 464.4 litres (16.25 cubic feet) measured at the normal temperature and pressure. This volume weighs 910 grams, or 14,105 grains.

If the expired air be measured as it leaves the Body its bulk will be found greater than that of the inspired air, since it not only has water vapor added to it, but is expanded in consequence of its higher temperature. If, however, it be dried and reduced to the same temperature as the inspired

air its volume will be found diminished, since it has lost 5.4 volumes per cent of oxygen and gained only 4.3 of carbon dioxide. In round numbers, 100 volumes of dry inspired air at zero, give 99 volumes of dry expired air measured at the same temperature and pressure.

Ventilation. Since at every breath some oxygen is taken from the air and some carbon dioxide given to it, were the atmosphere around a living man not renewed he would, at last, be unable to get from the air the oxygen he required; he would die of oxygen starvation or be *suffocated,* as such a mode of death is called, as surely, though not quite so fast, as if he were put under the receiver of an air-pump and all the air around him removed. Hence the necessity of ventilation to supply fresh air in place of that breathed, and clearly the amount of fresh air requisite must be determined by the number of persons collected in a room; the supply which would be ample for one person would be insufficient for two. Moreover fires, gas, and oil lamps, all use up the oxygen of the air and give carbon dioxide to it, and hence calculation must be made for them in arranging for the ventilation of a building in which they are to be employed.

In order that air be unwholesome to breathe, it is by no means necessary that it have lost so much of its oxygen as to make it difficult for the Body to get what it wants of that gas. The evil results of insufficient air-supply are rarely, if ever, due to that cause even in the worst-ventilated room for, as we shall see hereafter, the blood is able to take what oxygen it wants from air containing comparatively little of that gas. The headache and drowsiness which come on from sitting in a badly ventilated room, and the want of energy and general ill-health which result from permanently living in such, are dependent on a slow poisoning of the Body by the reabsorption of the things eliminated from the lungs in previous expirations. What these are is not accurately known; they doubtless belong to those volatile bodies mentioned above, as carried off in minute quantities in each breath; since observation shows that the air becomes injurious long before the amount of carbon dioxide in it is sufficient to do any harm. Breathing air containing one or two per cent of that gas produced by ordinary chemical methods does no particular injury, but breathing air containing one per cent of it produced by respiration is decidedly injurious,

because of the other things sent out of the lungs at the same time. Carbon dioxide itself, at least in any such percentage as is commonly found in a room, is not poisonous, as used to be believed, but, since it is tolerably easily estimated in air, while the actually injurious substances evolved in breathing are not, the purity or foulness of the air in a room is usually determined by finding the percentage of carbon dioxide in it: it must be borne in mind that to mean much this carbon dioxide must have been produced by breathing; the amount of it found is in itself no guide to the quantity of really important injurious substances present. Of course when a great deal of carbon dioxide is present the air is irrespirable: as for example sometimes at the bottom of wells or brewing-vats.

In one minute $.5 \times 15 = 7.5$ liters (0.254 cubic feet) of air are breathed and this is vitiated with carbon dioxide to the extent of rather more than four per cent; mixed with three times its volume of external air, it would give thirty liters (a little over one cubic foot) vitiated to the extent of one per cent, and such air is not respirable for any length of time with safety. The result of breathing it for an evening is headache and general malaise; of breathing it for weeks or months a lowered tone of the whole Body —less power of work, physical or mental, and less power of resisting disease; the ill effects may not show themselves at once, and may accordingly be overlooked, or considered scientific fancies, by the careless; but they are nevertheless there ready to manifest themselves. In order to have air to breathe in a fairly pure state every man should get for his own allowance at least 23,000 liters of space to begin with (about 800 cubic feet) and the arrangements for ventilation should, at the very least, renew this at the rate of 30 litres (one cubic foot) per minute. The nose is, however, the best guide, and it is found that at least five times this supply of fresh air is necessary to keep free from odor a small room inhabited by one adult. In the more recently constructed hospitals, as a result of experience, twice the above minimum cubic space is allowed for each bed in a ward, and the re-placement of the old air at a far more rapid rate is also provided for.

Ventilation does not necessarily imply draughts of cold air, as is too often supposed. In warming by indirect radia-

tion it may readily be secured by arranging, in addition to the registers from which the warmed air reaches the room, proper openings at the opposite side, by which the old air may pass off to make room for the fresh. An open fire in a room will always keep up a current of air through it, and is the healthiest, though not the most economical, method of warming an apartment.

Stoves in a room, unless constantly supplied with fresh air from without, dry its air to an unwholesome extent. If no appliance for providing this supply exists in a room, it can usually be got, without a draught, by fixing a board about four inches wide under the lower sash and shutting the window down on it. Fresh air then comes in by the opening between the two sashes and in a current directed upwards, which gradually diffuses itself over the room without being felt as a draught at any one point. In the method of heating by direct radiation, the apparatus employed provides of itself no means of drawing fresh air into a room, as the draught up the chimney of an open fireplace or of a stove does; and therefore special inlet and outlet openings are very necessary. Since few doors and windows, fortunately, fit quite tight, fresh air gets even into closed rooms, in tolerable abundance for one or two inhabitants, if there be outlets for the air already in them.

Changes undergone by the Blood in the Lungs. These are the exact reverse of those undergone by the breathed air —what the air gains the blood loses, and *vice versa.* Consequently, the blood loses heat, and water, and carbon dioxide in the pulmonary capillaries; and gains oxygen. These gains and losses are accompanied by a change of color from the dark purple which the blood exhibits in the pulmonary artery, to the bright scarlet it possesses in the pulmonary veins.

The dependence of this color change upon the access of fresh air to the lungs while the blood is flowing through them, can be readily demonstrated. If a rabbit be rendered unconscious by chloroform, and its chest be opened, after a pair of bellows has been connected with its windpipe, it is seen that, so long as the bellows are worked to keep up artificial respiration, the blood in the right side of the heart (as seen through the thin auricle) and that in the pulmonary artery, is dark colored, while that in the pulmonary veins

and the left auricle is bright red. Let, however, the artificial respiration be stopped for a few seconds and, consequently, the renewal of the air in the lungs (since an animal cannot breathe for itself when its chest is opened), and very soon the blood returns to the left auricle as dark as it left the right. In a very short time symptoms of suffocation show themselves and the animal dies, unless the bellows be again set at work.

The Blood Gases. If fresh blood be rapidly exposed to as complete a vacuum as can be obtained, it gives off certain gases, known as the *gases of the blood.* These are the same in kind, but differ in proportion, in venous and arterial blood; there being more carbon dioxide and less oxygen obtainable from the venous blood going to the lungs by the pulmonary artery, than from the arterial blood coming back to the heart by the pulmonary veins. The gases given off by venous and arterial blood, measured under the normal pressure and at the normal temperature, amount to from 58 to 62 volumes for every 100 volumes of blood, and in the two cases are about as follows—

	Venous Blood.	Arterial Blood.
Oxygen	10	20
Carbon dioxide	46	40
Nitrogen	2	2

It is important to bear in mind that while arterial blood contains some carbon dioxide that can be removed by the air-pump, venous blood also contains some oxygen removable in the same way; so that the difference between the two is only one of degree. When an animal is killed by suffocation, however, the last trace of oxygen which can be yielded up in a vacuum disappears from the blood before the heart ceases to beat. All the blood of such an animal is what might be called suffocation blood, and has a far darker color than ordinary venous blood.

The Cause of the Bright Color of Arterial Blood. The color of the blood depends on its red corpuscles, since pure blood plasma or blood serum is colorless, or at most a very faint straw yellow. Hence the color change which the blood experiences in circulating through the lungs must be due to some change in its red corpuscles. Now, minute solid bodies suspended in a liquid reflect more light when they are more dense, other things being equal; and the first thing that sug-

gests itself as the cause of the change in color of the blood is that its red corpuscles have shrunk in the pulmonary circulation, and so reflect more light and give the blood a brighter look. This idea gains some support from the fact that, as seen under the microscope, the red blood corpuscles of some animals, as the frog, do expand somewhat when exposed to carbon dioxide gas and shrink up a little in oxygen. But that this is not the chief cause of the color change is readily proved. By diluting blood with water the coloring matter of the red corpuscles can be made to pass out of them and go into solution in the plasma, and it is found that such a solution, in which there can be no question as to the reflecting powers of colored solid bodies suspended in it, is brighter red when supplied with oxygen than when deprived of that gas. This suggests that the coloring matter or *hæmoglobin* of the red corpuscles combines with oxygen to form a scarlet compound, and when deprived of that gas has a darker and more purple color; and other experiments confirm this. Hæmoglobin combined with oxygen is known as *oxyhæmoglobin,* and it is on its predominance that the color of arterial blood depends. Hæmoglobin uncombined with oxygen, sometimes named *reduced hæmoglobin,* predominates in venous blood, and is the only kind found in the blood of a suffocated mammal.

The Laws Governing the Absorption of Gases by a Liquid. In order to understand the condition of the gases in the blood liquid it is necessary to recall the general laws in accordance with which liquids absorb gases. They are as follows :

1. A given volume of a liquid at a definite temperature if it absorbs any of a gas to which it is exposed, and yet does not combine chemically with it, takes up a definite volume of the gas. If the gas be compressed the liquid will still, at the same temperature, take up the same volume as before, but now it takes up a greater weight; and a weight exactly as much greater as the pressure is greater, since one volume of a gas under any pressure contains exactly twice as much of the gas by weight as the same volume under half the pressure; and so on. A liter or a quart of water, for example, exposed to the air will dissolve a certain amount of oxygen. If the air (and therefore the oxygen in it) be compressed to one fourth its bulk then the water will dissolve exactly the

same volume of oxygen as before, but this volume of the compressed gas will contain exactly four times as much oxygen as did the same volume of the gas under the original pressure; and if, now, the pressure be again diminished the oxygen will be given off exactly in proportion as its pressure on the surface of the water decreases. Finally, when a complete vacuum is formed above the surface of the water, it will be found that the latter has given off all its dissolved oxygen. This law, that the quantity of a gas dissolved by a liquid varies directly as the pressure of that gas on the surface of the liquid is known as Dalton's law.

2. The amount of a gas dissolved by a liquid depends, not on the total pressure exerted by all the gases pressing on its surface, but on the fraction of the total pressure which is exerted by the particular gas in question. For example, the average atmospheric pressure is equal to that of a column of mercury 760 mm. (30 inches) high. But 100 volumes of air contain approximately 80 volumes of nitrogen and 20 of oxygen: therefore $\frac{1}{5}$ of the total pressure is due to oxygen and $\frac{4}{5}$ to nitrogen : and the amount of oxygen absorbed by water is just the same as if all the nitrogen were removed from the air and its total pressure therefore reduced to $\frac{1}{5}$ of 760 mm. (30 inches) of mercury; that is, to 152 mm. (6 inches) of mercury pressure. It is only the fraction of the total pressure exerted by the oxygen itself which affects the quantity absorbed by water at any given temperature. So, too, of all the atmospheric pressure $\frac{4}{5}$ is due to nitrogen, and all the oxygen might be removed from the air without affecting the quantity of nitrogen which would be absorbed from it by a given volume of water. The atmospheric pressure would then be $\frac{4}{5}$ of 760 mm. of mercury, or 608 mm. (24 inches), but it would all be due to nitrogen gas—and be exactly equal to the fraction of the total pressure due to that gas before the oxygen was removed from the air. When several gases are mixed together the fraction of the total pressure exerted by each one is known as the *partial pressure* of that gas; and it is this partial pressure which determines the amount of each individual gas dissolved by a liquid. If a liquid exposed to the air for some time had taken up all the oxygen and nitrogen it could at the partial pressures of those gases in the air, and were then put in an atmosphere in which the oxygen had all been replaced by nitrogen, it

would now give off all its oxygen, since, although the total gaseous pressure on it was the same, no part of it was any longer due to oxygen; and at the same time it would take up one fifth more nitrogen, since the whole gaseous pressure on its surface was now due to that gas, while before only four fifths of the total was exerted by it. If, on the contrary, the liquid were exposed to pure hydrogen under a pressure of one atmosphere it would give off all its previously dissolved oxygen and nitrogen, since none of the pressure on its surface would now be due to those gases; and would take up as much hydrogen as corresponded to a pressure of that gas equal to 760 mm. of mercury (30 inches).

3. A liquid may be such as to combine chemically with a gas. Then the amount of the gas absorbed is independent of the partial pressure of the gas on the surface of the liquid. The quantity absorbed will depend upon how much the liquid can combine with. Or, a liquid may partly be composed of things which simply dissolve a gas and partly of things which chemically combine with it. Then the amount of the gas taken up under a given partial pressure will depend on two things; a certain portion, that merely dissolved, will vary with the pressure of the gas in question; but another portion, that chemically combined, will remain the same under different pressures. The amount of this second portion depends only on the amount of the substance in the liquid which can chemically combine with it, and is totally independent of the partial pressure of the gas.

4. Bodies are known which chemically combine with certain gases when the partial pressure of these is considerable, forming compounds which break up, or *dissociate,* liberating the gas, when its partial pressure falls below a certain limit. Oxygen forms such a compound with hæmoglobin.

5. A membrane, moistened by a liquid in which a gas is soluble, does not essentially alter the laws of absorption, by a liquid on one side of it of a gas present on its other side, whether the absorption be due to mere solution or to chemical combinations or to both.

The Absorption of Oxygen by the Blood. Applying the physical and chemical facts stated in the preceding paragraph to the blood, we find that the blood contains (1) plasma, which simply dissolves oxygen, and (2) *hæmoglobin,*

which combines with it under some partial pressures of that gas, but gives it up under lower.

Blood plasma or, what comes to the same thing, fresh serum, exposed to the air, takes up no more oxygen than so much water: about 0.56 volumes of the gas for every 100 of the liquid, at a temperature of 20° C. At the temperature of the Body the volume absorbed would be still less. This quantity obeys Dalton's law.

If fresh whipped blood be employed, the quantity of oxygen taken up is much greater; this extra quantity must be taken up by the red corpuscles (in possessing which whipped blood alone differs from blood serum) and it does not obey Dalton's law. If the partial pressure of oxygen on the surface of the whipped blood be doubled, only as much more oxygen will be taken up as corresponds to that dissolved in the serum; and if the partial pressure of oxygen on its surface be reduced to one half, only a very small amount of oxygen (one half of that dissolved by the serum) will be given off. All the much larger quantity taken up by the red corpuscles will be unaffected and must therefore be chemically combined with something in them. Since 90 per cent of their dry weight is hæmoglobin, and this body when prepared pure is found capable of combining with oxygen, there is no doubt that it is the hæmoglobin in the circulating blood which carries around most of its oxygen. The red corpuscles are so many little packages in which oxygen is stowed away.

The compound formed between oxygen and hæmoglobin is, however, a very feeble one; the two easily separate, and always do so when the oxygen pressure in the liquid or gas to which the oxyhæmoglobin is exposed falls below 25 millimeters of mercury. Hence, in an air-pump, the blood only gives off some of its small portion of merely dissolved oxygen, until the pressure falls to about $\frac{1}{6}$ of an atmosphere, that is to $\frac{760}{6} = 125$ mm. (5 inches) of mercury, of which total pressure one fifth (25 millimeters or 1 inch) is due to the oxygen present. As soon as this limit is passed the hæmoglobin gives up its oxygen with a rush.

Consequences of the Peculiar Way in which the Oxygen of the Blood is Held. The first, and most important, is that the blood can take up far more oxygen in the lungs than would otherwise be possible. Since blood serum exposed to pure oxygen takes up only 3 volumes for 100, blood

exposed to the air would take up one fifth only of that amount at ordinary temperatures, and still less at the temperature of the Body, were it not for its hæmoglobin. In the lungs even less would be taken up, since the air in the air-cells of those organs is poorer in oxygen than the external air; and consequently the partial pressure of that gas in it is lower. The tidal air taken in at each breath serves merely to renew directly the air in the big bronchi; the deeper we examine the pulmonary air the less oxygen and more carbon dioxide would be found; in the layers farthest from the exterior and only renewed by diffusion with the air of the large bronchi, it is estimated that the oxygen only exists in such quantity that its partial pressure is equal to 130 millimeters of mercury, instead of 152 as in ordinary air. In the second place, on account of the way in which hæmoglobin combines with oxygen, the quantity of that gas taken up by the blood is independent of such variations of its partial pressure in the atmosphere as we are subjected to in daily life. At the top of a high mountain, for example, the atmospheric pressure is greatly diminished, but still mountaineers can breath freely and get all the oxygen they want; the distress felt for a time by persons unused to living in high altitudes is due mainly to circulatory disturbances resulting from the low atmospheric pressure. So long as the partial pressure of that gas in the lung air-cells is above 25 millimeters of mercury, the amount of it taken up by the blood depends on how much hæmoglobin there is in that liquid and not on how much oxygen there is in the air. So, too, breathing pure oxygen under a pressure of one atmosphere, or air compressed to one half or a fourth its normal bulk, does not increase the quantity of oxygen absorbed by the blood, apart from the small extra quantity dissolved by the plasma. The widespread statements as to the exhilaration caused by breathing pure oxygen are erroneous, being founded on experiments made with impure gas.

The General Oxygen Interchanges in the Blood. Suppose we have a quantity of arterial blood in the aorta. This, fresh from the lungs, will have its hæmoglobin almost fully combined with oxygen and in the state of oxyhæmoglobin. In the blood plasma some more oxygen will be dissolved, viz., so much as answers to a pressure of that gas equal to 130 mm. (5.2 inches) of mercury, which is the partial pressure of

oxygen in the pulmonary air-cells. This *tension* of the gas in the plasma will be more than sufficient to keep the hæmoglobin from giving off its oxygen. Suppose the blood now enters the capillaries of a muscle. In the liquid moistening this organ the oxygen tension is almost *nil,* since the tissue elements are steadily taking the gas up from the lymph around them. Consequently, through the capillary walls, the plasma will give off oxygen until the tension of that gas in it falls below 25 millimeters of mercury. Immediately some of the oxyhæmoglobin is decomposed, and the oxygen liberated is dissolved in the plasma, and from there next passed on to the lymph outside; and so the tension in the plasma is once more lowered and more oxyhæmoglobin decomposed. This goes on so long as the blood is in the capillaries of the muscle, or at any rate so long as the muscular fibres keep on taking oxygen from the lymph bathing them; if they cease to do so of course the tension of that gas in the lymph will soon come to equal that in the plasma: the latter will therefore cease to yield oxygen to the former; and so maintain its tension (by the oxygen received from the last decomposed oxyhæmoglobin) at a point which will prevent the liberation of any more oxygen from such red corpuscles as have not yet given all of theirs up. The blood will now go on as ordinary venous blood into the veins of the muscle and so back to the lungs. It will consist of (1) *plasma* with oxygen dissolved in it at a tension of about 25 millimeters (1 inch) of mercury. (2) A number of red corpuscles containing reduced hæmoglobin. (3) A number of red corpuscles containing oxyhæmoglobin. Or perhaps all of the red corpuscles will contain some reduced and some oxidized hæmoglobin. The relative proportion of reduced and unreduced hæmoglobin will depend on how active the muscle had been; if it worked while the blood flowed through it, it will have used up more oxygen, and the blood leaving it will consequently be more venous, than if it rested. This venous blood, returning to the heart, is sent on to the pulmonary capillaries. Here, the partial pressure of oxygen in the air-cells being 130 mm. (5.2 inches) and that in the blood plasma much less, oxygen will be taken up by the latter, and the tension of that gas in the plasma tend to be raised above the limit at which hæmoglobin combines with it. Hence, as fast as the plasma gets oxygen those red corpuscles which

contain any reduced hæmoglobin rob it, and so its oxygen tension is kept down below that in the air-cells until all the hæmoglobin is satisfied. Then the oxygen tension of the plasma rises to that of the gas in the air-cells; no more oxygen is absorbed, and the blood returns to the left auricle of the heart in the same condition, so far as oxygen is concerned, as when we commenced to follow it.

The Carbon Dioxide of the Blood. The same general laws apply to this as to the blood oxygen. The gas is partly merely dissolved and partly in a loose chemical combination much like that of oxygen with hæmoglobin, but the body with which it combines probably exists in the plasma more than in the red corpuscles; what it may be is not certainly known. Besides this, some more carbon dioxide is stably combined and is only given off on the addition of a stronger acid. The partial pressure of carbon dioxide in the pulmonary air-cells is about 40 mm. (1.6 inches) of mercury. Therefore the tension of that gas in the pulmonary capillaries must be more than this. On the other hand its tension in arterial blood must be less than that in the lymph around the tissues; otherwise it could not enter the blood in the systemic circulation, which it does, as proved by the fact that 100 vols. of venous blood give off 46 of this gas, and 100 vols. of arterial only 40.

The nitrogen dissolved in the blood is, so far as we know, quite unimportant.

Internal Respiration. As to the amount of oxygen used by each tissue and the quantity of carbon dioxide produced by it we know but little; the following points seem, however, tolerably certain:

1. The amount of carbon dioxide produced in an organ in a given time bears no constant ratio to the amount of oxygen taken up by it simultaneously. This is certainly true of muscle, for experiment shows that muscular work if really severe leads to an elimination of carbon dioxide containing more oxygen than the total oxygen taken up from the lungs at the same time. The balance is of course made up in subsequent periods of rest, when more free oxygen is taken up than is eliminated in combination during the same time. Moreover, a frog's muscle excised from the body and put in an atmosphere containing no oxygen and made there to contract, will evolve with each contraction considerable

quantities of carbon dioxide—although from the conditions of the experiment it can receive from outside no uncombined oxygen, and other experiments show that it contains none. Hence the living muscular fibre must contain a substance which is decomposed during activity and yields carbon dioxide as one product of decomposition; and this quite independent of any simultaneous direct oxidation.

2. What is true of muscle is probably true of most of the tissues. During rest they take up oxygen and fix it in the form of complex compounds, bodies which, like nitro-glycerine, are readily decomposed into simpler, and in such decompositions liberate energy which is used by the working tissue. One product of the decomposition is the highly oxidized carbon dioxide, and this is eliminated; other products are less oxidized, and possibly are not eliminated but built up again, with fresh oxygen taken from the blood and fresh carbon from the food, into the decomposable substance.

3. During the day a man gives off from his lungs more oxygen in carbon dioxide, than he takes up by the same organs from the air. During the night the reverse is the case. This, however, has nothing to do with the alternating periods of light and darkness, as it has in the case of a green plant, which in the light evolves more oxygen than it consumes, and in the dark the contrary. It depends, rather, on the fact that during the day more muscular effort is exerted than at night, and the meals are then taken and digested. The activity of the muscles and the digestive glands is dependent on processes which give rise to a large production of carbon dioxide and, during the night, when both are at rest, more oxygen is taken up than is contained in the carbon dioxide eliminated. If a man works and takes his meals at night, and sleeps in the day, the usual ratios of his gaseous exchanges with the exterior are entirely reversed.

4. The amount of work that a man's organs do, is not dependent on the amount of oxygen supplied to them, but the amount of oxygen used by him depends on how much he uses his organs. The quantity of oxygen supplied must of course always be, at least, that required to prevent suffocation; but an excess above this limit will not make the tissues work. Just as a man must have a certain amount of food to keep him alive, so he must have a certain amount of oxygen; but as extra food will not make his tissues or *him*

(who is physiologically the sum of all his tissues) work, apart from some stimulus to exertion, so it is with oxygen. Highly arterialized blood, or an abnormal amount of blood, flowing through an organ will not arouse it to activity; the working organ, muscle, or gland, for example, usually gets enough more blood to supply its extra needs—just as a healthy man who works will have a better appetite than an idle one; but as taking more food by an idle man will not of itself make him more energetic, so neither will sending more arterial blood through an organ excite it to activity.

5. The preceding statement is confirmed by experiments which show that an animal uses no more oxygen in an hour when made to breathe that gas in a pure state, than when allowed to breathe ordinary air. In other words, the amount of oxygen an animal uses (provided it gets the minimum necessary for health) is dependent only on how much it uses its tissues. These (the rest in most cases subject to a certain amount of control from the nervous) determine their own activity, and this, in turn, how much oxygen shall be used in the systemic circulation and restored in the pulmonary. In other words, the physiological work of an animal, which of course is largely dependent upon how external forces act upon it, determines how much oxygen it uses daily; and not the supply of oxygen how much its tissue activity shall be, unless the supply sinks below the starvation limit.

CHAPTER XXVII.

THE NERVOUS FACTORS OF THE RESPIRATORY MECHANISM. ASPHYXIA.

The Respiratory Centre. The respiratory movements are to a certain extent under the control of the will; we can breathe faster or slower, shallower or more deeply, as we wish, and can also " hold the breath " for some time—but the voluntary control thus exerted is limited in extent; no one can commit suicide by holding his breath. In ordinary quiet breathing the movements are quite involuntary; they go on perfectly without the least attention on our part, and, not only in sleep, but during the unconsciousness of fainting or of an apoplectic fit. The natural breathing movements are therefore either reflex or automatic.

The muscles concerned in producing the changes in the chest which lead to the entry or exit of air are of the ordinary striped kind; and these, as we have seen, only contract in the Body under the influence of the nerves going to them; the nerves of the diaphragm are the two phrenic nerves, one for each side of it; the external intercostal muscles are supplied by certain branches of the thoracic spinal nerves, called the intercostal nerves. If the phrenic nerves be cut the diaphragm ceases its contractions, and a similar paralysis of the external intercostals follows section of the intercostal nerves.

Since the inspiratory muscles only act when stimulated by nervous impulses reaching them, we have next to seek where these impulses originate; and experiment shows that it is in the *medulla oblongata*. All the brain of a cat or a rabbit in front of the medulla can be removed, and it will still go on breathing; and children are sometimes born with the medulla oblongata only, the rest of the brain being undeveloped, and yet they breathe for a time. If, on the other hand, the spinal cord be divided immediately below the medulla of an animal, all breathing movements of the

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chest cease at once. We conclude, therefore, that the nervous impulses calling forth contractions of the respiratory muscles arise in the medulla oblongata, and travel down the spinal cord and thence out along the phrenic and intercostal nerves. This is confirmed by the fact that if the spinal cord be cut across below the origin of the fourth pair of cervical spinal nerves (from which the phrenics mainly arise) but above the first thoracic spinal nerves, the respiratory movements of the diaphragm continue, but those of the intercostal muscles cease; this phenomenon has sometimes been observed on men so stabbed in the back as to divide the spinal cord in the region indicated. Finally, that the nervous impulses exciting the inspiratory muscles originate in the medulla, is proved by the fact that if a small portion of that organ, the so-called *vital point*, be destroyed, all the respiratory movements cease at once and forever, although all the rest of the brain and spinal cord may be left uninjured. This part of the medulla is known as the *respiratory centre*. The impulses proceeding from it probably do not pass directly to the motor nerve-fibres concerned, but first to subsidiary centres in the cord, from which properly co-ordinated impulses are sent to the muscles concerned. Occasionally in young animals, especially after a small dose of strychnia has been administered, a few respiratory movements are seen after section of the cord high up in the neck. But the broad general fact remains, that in the normal working of the Body the spinal respiratory centres only send out respiration-causing impulses when excited by impulses descending to them from the main respiratory centre in the medulla.

In the above statements, attention has been chiefly confined to the diaphragm and the intercostal muscles; but what is said of them is true of the respiratory innervation of all other breathing muscles, whether expiratory or inspiratory, normal or extraordinary.

Is the Respiratory Centre Reflex? Since this centre goes on working independently of the will, we have next to inquire is it a reflex centre or not ? are the efferent discharges it sends along the respiratory nerves due to afferent impulses reaching it by centripetal nerve-fibres? or does it originate efferent nervous impulses independently of excitation through afferent nerves?

We know, in the first place, that the respiratory centre is

largely under reflex control; a dash of cold water on the skin, the irritation of the nasal mucous membrane by snuff, or of the larynx by a foreign body, will each cause a modification in the respiratory movements—a long indrawn breath, a sneeze, or a cough. But, although thus very subject to influences reaching it by afferent nerves, the respiratory centre seems essentially independent of such. In many animals, as rabbits (and in some men), marked breathing movements take place in the nostrils, which dilate during inspiration; and when the spinal cord of a rabbit is cut close to the medulla, thus cutting off all afferent nervous impulses to the respiratory centre except such as may reach it through cranial nerves, the respiratory movements of the nostrils still continue until death. The movements of the ribs and diaphragm of course cease, and so the animal dies very soon unless artificial respiration be maintained. Moreover, if after cutting the spinal cord as above described, the chief sensory cranial nerves be divided, so as to cut off the respiratory centre from almost all possible afferent nervous impulses, the regular breathing movements of the nostrils continue. It is, therefore, nearly certain that the activity of the respiratory centre, however much it may be capable of modification through sensory nerves, is essentially independent of them; in other words the normal respiratory movements are not reflex.

What it is that Excites the Respiratory Centre. The thing that, above all others, influences the respiratory centre is the greater or less venosity of the blood flowing through it. If this blood be very rich in oxygen and comparatively poor in carbon dioxide the respiratory centre acts but feebly, and the respirations are shallow. If, on the other hand, this blood be highly venous the respiratory movements are more rapid than normal, and are forced, the extraordinary muscles of respiration being called into play; this state of violent labored respiration, due to deficient aëration of the blood is called *dyspnœa.* Normal quiet breathing is *eupnœa.* If active artificial respiration be kept up on an animal for a short time, it is found, on its cessation, that the creature (dog or rabbit) makes no attempt to breathe for a period which may extend to one and a half minutes. This breathless condition, in which an animal with no hindrance opposed to its breathing makes no respiratory movement, is *apnœa.*

Apnœa used to be ascribed solely to an overloading of the blood with oxygen, but the hæmoglobin of the blood leaving the lungs is normally so nearly saturated with that gas that this explanation is not sufficient. The apnœic state is in part due no doubt to the high percentage of oxygen in the air-cells of the lungs, brought about by the active artificial ventilation. The blood, as it flows through the lungs, is thus able to supply itself with oxygen for some time without any renewal of the air within them. But even this is not the whole matter, for an animal made apnœic will often continue so after its arterial blood has become distinctly venous in color; and an animal may, if its pneumogastric nerves be intact, be rendered apnœic for a short time by rapid insuffla-tion of its lungs with an indifferent gas. In fact, there is evidence that distention of the lungs tends to inhibit the sending out of impulses to the inspiratory muscles, the afferent fibres exerting this inhibitory action on the centre taking their course in the pulmonary branches of the pneu-mogastric; and this inhibition plays a part in the production of apnœa. It should be noted that by *apnœa* physicians usually mean only extreme dyspnœa.

How venous blood causes great excitation of the respira-tory centre is not certainly known. We may make the following provisional hypothesis: the chemical changes occurring in the respiratory centre produce a substance which stimulates its nerve-cells; when the blood is richly oxygenated this substance is oxidized as fast as it is formed, and the centre is not excited; but when the blood is poor in oxygen, the stimulating body accumulates and the respiratory discharges become powerful. Under normal circumstances the oxygen is not kept up to the point of entirely removing this exciting substance, and the centre is stimulated so as to produce the natural breathing movements. That the stimu-lant acts upon the respiratory centre itself, and not upon other organs of the Body and through their sensory nerves upon the medulla, is proved by experiments which show that the circulation of venous blood through the trunk and limbs of an animal, while its respiratory centre is supplied with arterial blood, does not produce dyspnœa.

Why are the Respiratory Discharges Rhythmic? Every complete respiratory act consists of an inspiration, an expira-tion and a pause; and then follows the inspiration of the

next act. In natural quiet breathing there is no essential difference between the expiration and the pause. The inspiration is the only active part; the expiration and the pause are dependent on muscular inactivity and, therefore, on the cessation of the discharge of nervous impulses from the respiratory centre. But then, we may ask, if in accordance with the hypothesis made in the last paragraph, the respiratory centre is constantly being excited, why is it not always discharging? why does it only send out nervous impulses at intervals? This question, which is essentially the same as that why the heart beats rhythmically, belongs to the higher regions of Physiology and can only at present be hypothetically answered. Let us consider, for a moment, ordinary mechanical circumstances under which a steady supply is turned into an intermittent discharge. Suppose a tube closed water-tight below by a hinged bottom, which is kept shut by a spring. If a steady stream of water is poured into the tube from above, the water will rise until its weight is able to overcome the pressure of the spring, and the bottom will then be forced down and some water flow out. The spring will then press the bottom up again, and the water accumulate until its weight again forces open the bottom of the tube, and there is another outrush; and so on. By opposing a certain resistance to the exit we could thus turn a steady inflow into a rhythmic outflow. Or, take the case of a tube with one end immersed in water and a steady stream of air blown into its other end. The air will emerge from the immersed end, not in a steady current, but in a series of bubbles. Its pressure in the tube must rise until it is able to overcome the cohesive force of the water, and then a bubble bursts forth; after this the air has again to get up the requisite pressure in the tube before another bubble is ejected; and so the continuous supply is transformed into an intermittent delivery. Physiologists suppose something of the same kind to occur in the respiratory centre. Its nerve-cells are always, under usual circumstances, being excited; but, to discharge a nervous impulse along the efferent respiratory nerves, they have to overcome a certain resistance. The nervous impulses have to accumulate, or "gain a head," before they travel out from the centre, and, after their discharge, time is required to attain once more the necessary level of irruption before a fresh in-

nervation is sent to the muscles. This method of accounting for the respiratory rhythm is known as the "*resistance theory.*" If not altogether satisfactory it is at least far preferable to the older mode of considering the question solved by assuming a rhythmic character or property of the respiratory centre. It gives a definite hypothesis, which accords with what is known of general natural laws outside of the Body, and the validity of which can be subjected to experiment: and so serves very well to show how scientific differs from pre-scientific, or mediæval, physiology. The latter was content with observing things in the Body and considered it explained a phenomenon when it gave it a name. Now we call a phenomenon explained, when we have found to what general category of natural laws it can be reduced as a special example; and this reducing a special case to a particular manifestation of some one or more general properties of matter already known is, of course, all that we ever mean when we say we explain anything. We explain the fall of an apple and the rise of the tides by referring them to the class of general results of the law of gravitation; but the why of the law of gravitation we do not know at all; it is merely a fact which we have found out. So with regard to Physiology; we are working scientifically when we try to reduce the activities of the living Body to special instances of mechanical, physical, or chemical laws otherwise known to us, and unscientifically when we lose sight of that aim. Certain vital phenomena, as those of blood-pressure, we can thus explain, as much as we can explain anything; others, as the rhythm of the respiratory movements, we can provisionally explain, although not yet certain that our explanation is the right one; and still others, as the phenomena of consciousness, we cannot explain at all, and possibly never shall, by referring them to general properties of matter, since they may be associated only with that particular kind of matter called protoplasm, and perhaps only with some varieties of it.

The Relation of the Pneumogastric Nerves to the Respiratory Centre. We have next to consider if any phenomena presented by the living Body give support to the resistance theory of the respiratory rhythm. A very important collateral prop to it is given by the relation of the pneumogastric nerves to the rate and force of the respiratory move-

ments. These nerves give branches to the larynx, the wind-pipe, and the lungs, and might therefore be suspected to have something to do with breathing. Indeed at one time it was maintained that the breathing movements were purely reflex, the afferent fibres running in the pneumogastrics from the lungs to the respiratory centre. That the vagi are not concerned in influencing the respiratory muscles directly is shown by the fact that all of these muscles (except certain small ones in the larynx) contract as usual in breathing after both pneumogastric nerves have been divided. Still, the section of both nerves has a considerable influence on the respiratory movements; they become *slower and deeper*. We may understand this by supposing that the resistance to the discharges of the respiratory centre is liable to variation. It may be increased, and then the discharges will be fewer and larger; or diminished, and then they will be more frequent but each one less powerful. If the spring, in the illustration used in the preceding paragraph, be made stronger, while the inflow of water to the tube remains the same, the outflows will be less frequent but each one greater; and *vice versa*. The effect of section of the pneumogastric trunk may, therefore, be explained if we suppose that, normally, it carries up, from its lung branches, nervous impulses which diminish the resistance to the discharges of the respiratory centre; when the nerves are cut these helping impulses are lost to the centre, and its impulses must gather more head before they break out, but will be greater when they do. This view is confirmed by the fact that stimulation of the central ends of the divided pneumogastrics, if weak, brings back the respirations to their normal rate and force; if stronger makes them more rapid and shallower; and when stronger still, abolishes the respiratory rhythm altogether, with the inspiratory muscles in a steady state of feeble contraction. That is to say, the resistance to the discharges of the centre being entirely taken away (which is equivalent to the total removal of the spring in our example), the centre sends out uninterrupted and non-rhythmic stimuli to the inspiratory muscles.

The pneumogastric nerve gives two branches to the larynx; known respectively as the *superior* and *inferior (recurrent) laryngeal* nerves; the action of these on the respiratory centre is opposite to that of the fibres from the lungs

coming up in the main pneumogastric trunk. If the superior laryngeal branch be divided and its central end stimulated, the respirations become less frequent but each one more powerful; hence this nerve appears to contain fibres which increase the resistance to inspiratory discharges from the respiratory centre. The same, but to a less degree, is true of the inferior laryngeal branch. Both are inhibitory fibres so far as inspiration is concerned; whereas the main vagus stem when its central end is electrically stimulated is accelerator or augmentor.

The Expiratory Centre. Hitherto we have considered breathing as due to the rhythmically alternating activity and rest of an inspiratory centre—and such is the case in normal quiet breathing, in which the expirations are passive. But in dyspnœa expiration is a muscular act, and so there must be a section of the respiratory centre controlling the expiratory muscles, and we may regard the whole centre as consisting really of two; an *inspiratory* and *expiratory*. The latter part of the respiratory centre, however, is less irritable than the inspiratory part, and hence when the blood is in a normal state of aëration never gets stimulated up to the discharging point. In dyspnœa the stimulus becomes sufficient to cause it also to discharge, but only after the more irritable inspiratory centre; hence the expiration follows the inspiration. This alternation of activity is, moreover, promoted by the fact that the pneumogastric nerve-fibres coming up from the lungs are of two kinds. The predominant sort are the accelerator set already referred to, which favor discharge of the inspiratory centre, and perhaps also increase the resistance to the expiratory discharge. This set is excited when the lungs diminish in bulk, as in expiration; and when the whole nerve is stimulated electrically they usually get the better of the other set, which carry up to the medulla impulses which inhibit inspiratory discharges. This set is stimulated by expansion of the lungs, even in quiet breathing: and they play a part in producing the phenomenon of *apnœa*. When the distention of the lungs is considerable these fibres not only check inspiration but favor expiratory movements. Hence, every expansion of the lungs (inspiration) tends to promote an expiration, and every collapse of the lungs (expiration) tends to produce an inspira-

tion; and so, through the pneumogastric nerves, the respiratory mechanism is largely self-regulating.

Asphyxia. Asphyxia is death from suffocation, or want of oxygen by the tissues. It may be brought about in various ways; as by strangulation, which prevents the entry of air into the lungs; or by exposure in an atmosphere containing no oxygen; or by putting an animal in a vacuum; or by making it breathe air containing a gas which has a stronger affinity for hæmoglobin than oxygen has, and which, therefore, turns the oxygen out of the red corpuscles and takes its place. The gases which do the latter are very interesting since they serve to prove conclusively that the Body can only live by the oxygen carried round by the hæmoglobin of the red corpuscles; that amount dissolved in the blood plasma being insufficient for its needs. Of such gases carbon monoxide is the most important and best studied; in the frequent French mode of committing suicide by stopping up all the ventilation holes of a room and burning charcoal in it, it is poisoning by carbon monoxide which causes death.

The Relations of Carbon Monoxide to Hæmoglobin. If aërated whipped blood, or a solution of oxyhæmoglobin, be exposed to a gaseous mixture containing carbon monoxide, the liquid will absorb the latter gas and give off oxygen. The amount of carbon monoxide taken up will (apart from a small amount dissolved in the plasma) be independent of the partial pressure of that gas in the gaseous mixture to which the blood is exposed; the quantity absorbed depends on the quantity of hæmoglobin in the liquid, and is replaced by an equal volume of oxygen liberated. This equivalence of volume, of itself, proves that the phenomenon is due to the chemical replacement of oxygen in some compound, by the carbon monoxide; for if the carbon monoxide were merely dissolved in the liquid in proportion to its partial pressure on the surface, it would turn out no oxygen; the quantity of dissolved gases held by a liquid being dependent only on the partial pressure of each individual gas on its surface, and unaffected by that of all others. During the taking up of carbon monoxide the blood changes color in a way that can be recognized by a practised eye; it becomes cherry-red instead of scarlet. This shows that some new chemical compound has been formed in it; examination with the spectroscope confirms this, and shows the color change to be due to

the formation of carbon-monoxide hæmoglobin which has a different color from oxyhæmoglobin. A dilute solution of reduced hæmoglobin absorbs all the rays of light in one region about the green of the solar spectrum, and so produces there a dark band; a thin layer of the blood of an asphyxiated animal does the same. Dilute solution of oxy-hæmoglobin absorbs the rays in two narrow regions of the solar spectrum at the confines of the yellow and green, and arterial blood does the same. Dilute solution of carbon-monoxide hæmoglobin, or blood which has been exposed to this gas, also absorbs the light in two narrow bands of the solar spectrum; but these are a little nearer the blue end of the spectrum than the absorption bands of oxyhæmoglobin. Pure blood serum saturated with oxygen gas or with carbon monoxide does not specially absorb any part of the spectrum; therefore the absorptions when hæmoglobin is present must be due to chemical compounds of those gases with that body.

Since carbon-monoxide hæmoglobin has a bright-red color, we find, in the Bodies of persons poisoned by that gas, the blood all through the Body cherry-red; the tissues being unable to take carbon monoxide from hæmoglobin in the systemic circulation. Hence the curious fact that, while death is really due to asphyxia, the blood is almost the color of arterial blood, instead of very dark purple, as in ordinary cases of death by suffocation. Experiments with animals show that in poisoning by carbon monoxide persistent exposure of the blood to oxygen, by means of artificial respiration, will cause the poisonous gas to be slowly replaced again by oxygen; hence if the heart has not yet quite stopped beating, artificial respiration, kept up patiently, should be employed in the case of poisoning by carbon monoxide unless transfusion of blood be possible.

The Phenomena of Asphyxia. As soon as the oxygen in the blood falls below the normal amount the breathing becomes hurried and deeper, and the extraordinary muscles of respiration are called into activity. The dyspnœa becomes more and more marked, and this is especially the case with the expirations which, almost or quite passively performed in natural breathing, become violently muscular. At last nearly all the muscles in the Body are set at work; the rhythmic character of the respiratory acts is lost, and general convulsions occur, but, on the whole, the contractions of the

expiratory muscles are more violent than those of the inspiratory. Thus undue want of oxygen at first merely brings about an increased activity of the respiratory centre, and especially of its expiratory division which is not excited in normal breathing. Then it stimulates other portions (the *convulsive centre*) of the medulla oblongata also, and gives rise to violent and irregular muscular spasms. That the convulsions are due to excitation of nerve-centres in the medulla (and not, as might be supposed, to poisoning of the muscles or of the fore parts of the brain by the extremely venous blood) is shown of the facts (1) that they do not occur in the trunk of an animal when the spinal cord has been divided in the neck so as to cut off the muscles from the medulla; and (2) that they still occur if (the spinal cord remaining undivided) all the parts of the brain in front of the medulla have been removed.

The violent excitation of the nerve-centres soon exhausts them, and all the more readily since their oxygen supply (which they like all other tissues need in order to continue their activity) is cut off. The convulsions therefore gradually cease, and the animal becomes calm again, save for an occasional act of breathing when the oxygen want becomes so great as to lead to efficient stimulation even of the dying respiratory centre: these final movements are inspirations and, becoming less and less frequent, at last cease, and the animal appears dead. Its heart, however, though gorged with extremely dark venous blood still makes some slow feeble pulsations. So long as it beats artificial respiration can restore the animal, but once the heart has finally stopped restoration is impossible. There are thus three distinguishable stages in death from asphyxia. (1) The stage of dyspnœa. (2) The stage of convulsions. (3) The stage of exhaustion; the convulsions having ceased but there being from time to time an inspiration. The end of the third stage occurs in a mammal about five minutes after the oxygen supply has been totally cut off. If the asphyxia be due to deficiency, and not absolute want of oxygen, of course all the stages take longer.

Circulatory Changes in Asphyxia. During death by suffocation characteristic changes occur in the working of the heart and blood-vessels. The heart at first beats quicker, but very soon, before the end of the dyspnœic stage, more

slowly, though, at first, more powerfully. This slowing is due to the fact that the unusual want of oxygen leads to stimulation of the cardio-inhibitory centre in the medulla and this, through the pneumogastric nerves, slows the heart's beat. Soon, however, the want of oxygen affects the heart itself and it begins to beat more feebly, and also more slowly, from exhaustion, until its final stoppage. During the second and third stages the heart and the venæ cavæ become greatly overfilled with blood, because the violent muscular contractions facilitate the flow of blood to the heart, while its beats become too feeble to send it out again. The overfilling is most marked on the right side of the heart which receives the venous blood from the Body generally.

During the first and second stages of asphyxia arterial pressure rises in a marked degree. This is due to excitation of the vaso-motor centre by the venous blood, and the consequent constriction of the muscular coats of the arteries and increase of the peripheral resistance. In the third stage the blood-pressure falls very rapidly, because the feebly acting heart then fails to keep the arteries tense, even although their diminished calibre greatly slows the rate at which they empty themselves into the capillaries.

Another medullary centre unduly excited during asphyxia is that from which proceed the nerve-fibres governing those muscular fibres of the eye which enlarge the pupil. During suffocation, therefore, the pupils become widely dilated. At the same time all reflex irritability is lost, and touching the eyeball causes no wink; the reflex centres all over the Body being rendered, through want of oxygen, incapable of activity. The same is true of the higher nerve-centres; unconsciousness comes on during the convulsive stage, which, horrible as it looks, is unattended with suffering.

Modified Respiratory Movements. *Sighing* is a deep long-drawn inspiration followed by a shorter but correspondingly large expiration. *Yawning* is similar, but the air is mainly taken in by the mouth instead of the nose, and the lower jaw is drawn down in a characteristic manner. *Hiccough* depends upon a sudden contraction of the diaphragm, while the aperture of the larynx closes; the entering air, drawn through the narrowing opening, causes the peculiar sound. *Coughing* consists of a full inspiration followed by a violent and rapid expiration, during the first part of which

the laryngeal opening is kept closed; being afterwards suddenly opened, the air issues forth with a rush, tending to carry out with it anything lodged in the windpipe or larynx. *Sneezing* is much like coughing, except that, while in a cough the isthmus of the fauces is held open and the air mainly passes out through the mouth, in sneezing the fauces are closed and the blast is driven through the nostrils. It is commonly excited by irritation of the nasal mucous membrane, but in many persons a sudden bright light falling into the eye will produce a sneeze. *Laughing* consists of a series of short expirations following a single inspiration; the larynx is open all the time, and the vocal cords (Chap. XXXVII.) are set in vibration. *Crying* is, physiologically, much like laughing and, as we all know, one often passes into the other. The accompanying contractions of the face muscles giving expression to the countenance are, however, different in the two.

All these modified respiratory acts are essentially reflex and they serve to show to what a great extent the discharges of the respiratory centre can be modified by afferent nerve impulses; but, with the exception of hiccough, they are to a certain extent, like natural breathing, under the control of the will. Most of them, too, can be imitated more or less perfectly by voluntary muscular movements; though a good stage sneeze or cough is rare.

CHAPTER XXVIII.

THE KIDNEYS AND SKIN.

General Arrangement of the Urinary Organs. These consist of (1) the *kidneys*, the glands which secrete the urine; (2) the *ureters* or ducts of the kidneys, which carry their secretion to (3) the *urinary bladder*, a reservoir in which it accumulates and from which it is expelled from time to time through (4) an exit tube, the *urethra*. The general arrangement of these parts, as seen from behind, is represented in Fig. 132. The two kidneys, *R*, lie in the dorsal part of the lumbar region of the abdominal cavity, one on each side of the middle line. Each is a solid mass, with a convex outer and a concave inner border, and its upper end a little larger than the lower. From the abdominal aorta, *A*, a *renal artery*, *Ar*, enters the inner border of each kidney, to break up within it into finer branches, ultimately ending in capillaries. The blood is collected from these into the *renal veins*, *Vr*, one of which leaves each kidney and opens into the inferior vena cava, *Vc*. From the concave border of each kidney proceeds also the *ureter*, *U*, a slender tube from 28 to 34 cm. (11 to 13.5 inches) long, opening below into the bladder, *Vu*, on its dorsal aspect, and near its lower end. From the bladder proceeds the urethra, at *Ua*. The channel of each ureter passes very obliquely through the wall of the bladder to open into it; accordingly if the pressure inside the latter organ rises above that of the liquid in the ureter, the walls of the oblique passage are pressed together and it is closed. Usually the bladder, which has a thick coat of unstriped muscular tissue lined by a mucous membrane, is relaxed, and the urine flows readily into it from the ureters. While urine is collecting, the beginning of the urethra is kept closed, in part at least, by bands of elastic tissue around it: some of the muscles which surround the commencement of the urethra assist, being kept in reflex contraction ; it is found that in a dog the urinary

bladder can retain liquid under considerably higher pressure when the spinal cord is intact than after destruction of its

R

U

Fig. 182.—The renal organs, viewed from behind. *R*, right kidney; *A*, aorta; *Ar*, right renal artery; *Vc*, inferior vena cava; *Vr*, right renal vein; *U*, right ureter; *Vu*, bladder; *Ua*, commencement of urethra.

lumbar portion. The contraction of these urethra-constricting muscles can be reinforced voluntarily. When some amount of urine has accumulated in the bladder, it contracts

and presses on its contents; the ureters being closed in the way above indicated, the elastic fibres closing the urethral exit are overcome, and the urethral muscles simultaneously relaxing, the liquid is forced out.

Naked Eye Structure of the Kidneys. These organs have externally a red-brown color, which can be seen through the transparent *capsule* of peritoneum which envelops them. When a section is carried through a kidney from its outer to its inner border (Fig. 133) it is seen that a deep fissure, the *hilus*, leads into the latter. In the *hilus* the ureter widens out to form the *pelvis, D,* which breaks up again into a number of smaller divisions, the cups or *calices.* The cut surface of the kidney proper is seen to consist of two distinct parts; an outer or *cortical portion,* and an inner or *medullary.* The medullary portion is less red and more glistening to the eye, is finely striated in a radial direction, and does not consist of one continuous mass but of a number of conical portions, the *pyramids of Malpighi, 2',* each of which is separated from its neighbors by an inward prolongation, *, of the cortical substance: this, however, does not reach to the inner end of the pyramid, which projects, as the *papilla,* into a calyx of the ureter. At its outer end each pyramid separates into smaller portions, the *pyramids of Ferrein, 2'',* separated by thin layers of cortex and gradually spreading everywhere into the latter. The cortical substance is redder and more granular looking and less shiny than the medullary, and forms everywhere the outer layer of the organ next its capsule, besides dipping in between the pyramids in the way described.

The renal artery divides in the hilus into branches (5) which run into the kidney between the pyramids, giving off a few twigs to the latter and ending finally in a much richer vascular network in the cortex. The branches of the renal vein have a similar course.

The Minute Structure of the Kidney. The kidneys are compound tubular glands, composed essentially of branched microscopic *uriniferous tubules,* lined by epithelium. Each tubule commences at a small opening on a papilla and from thence has a very complex course to its other extremity: usually about twenty open, side by side, on one papilla, where they have a diameter of about 0.125 mm. ($\frac{1}{200}$ inch). Running from this place into the pyramid

each tubule divides several times. At first the branches are smaller than the main tube; but as soon as they have come down to about 0.04 mm. ($\frac{1}{600}$ inch) this diminution in size ceases, and division continuing while the tubules retain the same diameter, the pyramid thus gets, in part, its conical form. Ultimately each branch runs out of the pyramid somewhere, either from its base or side, into the cortex and there dilates

Fig. 183.—Section through the right kidney from its outer to its inner border. 1, cortex; 2, medulla; 2', pyramid of Malpighi; 2'', pyramid of Ferrein; 3, small branches of the renal artery entering between the pyramids: A, a branch of the renal artery; D, the pelvis of the kidney; U, ureter; C, a calyx.

and is twisted. It then narrows and doubles back into one of the pyramids of Ferrein and runs as a straight tube towards the papilla, but before reaching it makes a loop (*loop of Henle*), and turns back again as a straight tube towards the base of the pyramid, where it once more enters the cortex, dilates and becomes contorted, and then ends in a spherical capsule,

containing a tuft of small blood-vessels. Or, followed the other way, each tubule commences in the cortex with a globular dilatation, the *Malpighian capsule.* From this it continues as a convoluted tubule in the cortex; this passes into a pyramid of Ferrein, becomes straight, and runs to near a pyramid of Malpighi as the *descending limb* of a *loop of Henle.* Turning at the loop, it continues as its *ascending limb,* and this passes out again into the cortex and becomes the convoluted *junctional tubule,* which passes as a straight *collecting tubule* into a pyramid of Ferrein, where it joins others to form an *excretory tubule;* the excretory tubules run into the main pyramid and unite to form the *discharging tubules* which open on the papilla. Throughout its course the tubule is lined by a single layer of epithelium cells differ-ing in character in its different sections: they are flat and clear in the capsules, and very granular in both the convoluted parts, where their appearance suggests that they are not mere lining cells but cells with active work to do; they are non-granular and flat in the descending limb of the loop of Henle, clear and columnar in most of the ascending, and in both are probably only protective; in the collecting and discharging tubules they are somewhat cuboidal in form and have no active secretory function. All the tubes are bound together by a sparse amount of connective tissue and by blood-vessels to form the gland. The lymph spaces are large and numerous, especially about the convoluted portions of the tubules.

The Blood-flow through the Kidney. The amount of blood brought to the kidney is large relatively to the size of the organ and enters under a very high pressure almost direct from the aorta, and leaves under a very low, into the inferior cava (Fig. 132). The final twigs of the renal artery in the cortex, giving off a few branches which end in a capillary network around the convoluted tubules and in the pyramids, are continued as the *afferent vessels* of Malpighian capsules, the walls of which are doubled in before them (Fig. 134); there each breaks up into a little knot of capillary vessels called the *glomerulus,* from which ultimately an *efferent vessel* proceeds. Where the wall of the glomerulus, *w,* Fig. 134, is doubled in before the blood-vessels, its lining cells continue as a covering, *c,* to the latter, closely adhering to the vascular walls. A space, *A,* is left between the epithelial cells of the

outside of the capsule and those involuted on the vessels, as there would be in the interior of a rubber ball one side of which was pushed in so as to nearly meet the other; this cleft, into which any liquid transuded from the vessels must enter, opens by a narrow *neck, d*, into the commencement of the first contorted part of an uriniferous tubule. The efferent vein, carrying blood away from the glomerulus, breaks up into a close capillary network around the neighboring tubules of the cortex. From these capillaries the blood is collected into the renal vein. Most of the blood flowing through the kidney thus goes through two sets of capillaries; one found in the capsules, and the second formed by the breaking up of their efferent veins. The capillary network in the pyramids is much less close than that in the cortex, which gives reason to suspect that most of the secretory work of the kidneys is done in the capsules and convoluted tubules. The pyramidal blood flows only through one set of capillaries, there being no glomeruli in the kidney medulla.

Fig. 134 – Diagram showing a kidney glomerulus and the commencement of an uriniferous tubule. *a*, afferent blood-vessel pushing in the wall, *w*, of a Malpighian capsule and ending in the capillary tuft from which the vein *e* issues: *c*, involuted epithelium covering the vascular tuft, for the sake of distinctness it is represented as a general wrapping for the whole tuft, but in nature it forms a close investment around each vessel of the glomerulus: *A*, space in capsule into which liquid transuded from the vessels of the glomerulus passes; *d*, neck of capsule passing into commencement of first convoluted portion, *ff*, of an uriniferous tubule: *o*, granular epithelial cells; *b*, basement membrane.

The Renal Secretion. The amount of this carried off from the Body in 24 hours is subject to considerable variation, being especially diminished by anything which promotes perspiration, and increased by conditions, as cold to the surface, which diminish the skin excretion. Its average daily quantity varies from 1200 to 1750 cub. cent. (40 to 60 fluid ounces). The urine is a clear amber-colored liquid, of a slightly acid reaction; its specific gravity is about 1022, being higher when the total quantity excreted is small than when it is greater, since the amount of solids dissolved in it remains nearly the same in health; the changes in its bulk being dependent mainly on changes in the amount of water separated from the blood by the kidneys.

Normal urine consists, in 1000 parts, of about 960 water and 40 solids. The latter are mainly crystalline nitrogenous bodies (*urea* and *uric acid*), but small quantities of pigments and of non-nitrogenous organic bodies are also present, and a considerable quantity of mineral salts. The following table gives approximately, in the first column, the average composition of the urine excreted in twenty-four hours expressed in grams; in the second column the same expressed in grains. The third column gives the composition of 1000 parts of urine.

Urine in 24 hours.	1500 grams.	23,250 grains.	In 1000 parts.
Water...............................	1428.00	22,184.00	952.00
Solids	72.00	1116.00	48.00
The solids consist of—			
Urea..........................	33.00	511.50	22.00
Uric acid......................	0.50	7.75	0.33
Hippuric acid.................	0.40	6.20	0.27
Kreatinin.....................	1.00	15.50	0.67
Pigments and fats............	10.00	155.00	6 66
Sulphuric acid....., ...	2.00	31.00	1.33
Phosphoric acid	3.00	46.50	2 00
Chlorine......................	7.00	108 50	4 67
Ammonia......................	0.75	12.00	0.50
Potassium.....................	2.50	38.75	1.67
Sodium........................	11.00	170.50	7.33
Calcium	0.25	3.80	0.17
Magnesium....................	0.20	3.00	0.13
	71.60	1110.00	47.73

The urine, however, even in health is subject to considerable variation in composition; not only as regards the amount of water in it, but also in respect to its solid constituents; the latter are especially modified by the quantity and nature of the food taken.

The Crystalline Nitrogenous Constituents of the Urine are of great interest as they represent the final result of the breaking down in the Body of albuminous and gelatinaginous substances, whether due to tissue waste or to the destruction in the bodily liquids of proteids and albuminoids existing in them in solution. Their chemical relationships tend to cast some light on the structure of an albumen molecule and on the metabolisms it undergoes in the living organism.

Urea (N_2H_4CO) is the chief nitrogenous waste product of the human Body and is related to the ammonia group, being readily converted into ammonium carbonate by hydration, a change which occurs under the influence of some living ferments when stale urine becomes alkaline and acquires its well-known offensive ammoniacal odor—

$$N_2H_4CO + 2H_2O = (NH_4)_2CO_3.$$
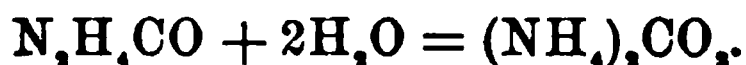
On another side urea is allied to the cyanogen group of substances, being isomeric with ammonium cyanate, which is converted into it by simple heating.

Uric acid ($C_5H_4N_4O_3$) is present in but small quantity in normal human urine, but is the chief nitrogenous excretion of birds and reptiles. Its molecular structure is more complex than that of urea, and when it is decomposed by various methods urea is very frequently one of the products. It is a less complete product of proteid degradation than urea. Some of its decompositions indicate relations to oxalic acid and to amido-acetic acid (*glycin*), and through this latter to the ammonias and the fatty acids series. In human urine uric acid exists chiefly in the form of salts of potassium and sodium; these are less soluble in cold than in warm water, and are sometimes deposited as a flocculent precipitate when originally clear urine is left to cool. The precipitate disappears on reheating the liquid.

Hippuric acid ($C_9H_9O_3$) is scanty in normal human urine but abundant in the urine of herbivora. Chemically it is related to the aromatic series, being formed when benzoic acid and glycin are made to unite with dehydration; and it is broken up into those substances when boiled with mineral acids. Certain aromatic bodies allied to benzoic acid are found in hay and similar foods and account for the large amount of hippurates in herbivorous urine. But proteids when broken up by putrefaction also yield bodies of the benzoic group, and the hippuric acid of human urine probably has its origin in the liberation of benzoic residues in metabolic activities of some of the living cells of the Body; these residues being then combined with glycin to form hippuric acid. That glycin is formed in the Body is shown by the fact that benzoic acid given in food reappears in human urine as hippuric acid, having been somewhere united to a glycin residue.

Kreatinin ($C_4H_7N_3O$) is closely allied to kreatin ($C_4H_9N_3O_2$), of which it is a simple dehydration product. Kreatin is a normal constituent of muscle (0.2-0.3%), being, indeed, most conveniently prepared from Liebig's extract; it is also known that kreatin introduced into the Body is converted into kreatinin; for if given in the food it causes an equivalent increase of the kreatinin excreted in the urine. Kreatin formed in the muscles has accordingly been supposed to be a source of the kreatinin of the urine, but this does not appear to be the case, as all kreatinin disappears from the urine during starvation. The kreatinin of normal urine probably has its source in the kreatin of flesh eaten as food.

The Urinary Pigments are still very imperfectly known, but appear in part to be derived from uro-bilin, which, as we have seen (Chap. XXIV), is itself probably a derivative of hæmoglobin.

Of the inorganic salts *sodium chloride* is by far the most abundant, but the *phosphates* deserve notice because the acidity of normal fresh urine is dependent on the presence of acid sodium phosphate.

In various diseases abnormal substances are found in the urine: the more important are albumens in *albuminuria* or Bright's disease; grape sugar or glucose in *diabetes;* bile salts ; bile pigments.

The Secretory Actions of Different Parts of an Uriniferous Tubule.—The microscopic structure of the kidneys is such as to suggest that in those organs we have to do with two essentially distinct secretory apparatuses: one represented by the glomeruli, with their capillaries separated only by a single layer of flat epithelial cells from the cavity of the capsule and especially adapted for filtration and dialysis; the other represented by the contorted portions of the tubules, with their large granular cells, which clearly have some more active part to play than that of a mere passive transudation membrane. And we find in the urine substances which like the water and mineral salts may easily be accounted for by mere physical processes, and others, urea especially, which are present in such proportion as must be due to some active physiological work of the kidney, whether a merely selective activity of its cells or a constructive one. More direct evidence does, in fact, justify us in saying that in general the glomeruli are transudation organs, the contorted portions of

the tubuli secretory organs, while the loops of Henle and the collecting and discharging tubules are merely passive channels for the gathering and transmission of liquid. Even in the glomeruli, however, the renal cells provide something more than a merely passive physical membrane for dialysis and filtration: to a certain extent they control the passage of substances through them; while they are in health no serum albumen or paraglobulin passes through them into the urine, though egg albumen injected into the blood of a living mammal does. But when they are altered in disease or even by a temporary stoppage of their blood-supply, then they allow the normal blood proteids to transude: if the blood-supply of a kidney be cut off for some minutes by clamping the renal artery, then the urine secreted for some time after the clamp is removed is albuminous.

The structure of the glomerular epithelium and its relation to the blood-vessels are such as to make it almost certain that when albumen appears in the urine it enters through them and not through other parts of the tubule; but in some amphibia we get direct evidence of the entry of substances other than salts and water into the renal secretion by the path of the Malpighian capsules. In amphibia the blood carried to the kidney, like that supplying the mammalian liver, has two sources, one venous and one arterial; the arterial supply comes from the renal arteries, the venous from the veins of the leg by the *reniportal vein*. Both bloods leave the organ by the renal veins, but their distribution in it is in great part distinct; the arteries supply the glomeruli, the reniportal vein the tubules of the cortex, though mixed there with blood from the efferent vessels of the glomeruli. In some small amphibia it is, in fact, possible to observe the circulation in the living kidney and to see that all blood-flow in the glomeruli ceases when the renal arteries are tied, though it continues elsewhere throughout the organ. When sugar or peptone is injected into the blood of such an animal those substances appear in the urine; but if the renal arteries be previously tied they do not. It is true that under those circumstances all secretion of urine usually ceases, but it may be excited by administering certain drugs, and then is found to be free from sugar and peptone. Grape-sugar when present in the blood of mammals beyond a certain small percentage passes out in the urine; and the same is true of peptone:

indeed, the absence of peptone (or of all but the merest traces of it) from healthy human urine is one of the main reasons for believing that peptone absorbed from the alimentary canal is converted at once by the lymphoid tissues of the mucous membrane into the proper proteids of the blood plasma. When sugar appears in the urine either in disease or, as sometimes happens temporarily, in health, after a meal rich in starchy substances we have from the results of experiment on amphibia reason to believe that its path of excretion is through the glomeruli. In *hæmoglobinuria*, a condition in which hæmoglobin is found in solution in urine (not in blood-corpuscles, for in that case it may have come from ruptured vessels anywhere in the renal apparatus), the hæmoglobin also passes out through the Malpighian bodies: for when some laky blood (Chap. IV) is injected into the vessels of an animal and the secretion of urine at the same time made slow, collections of hæmoglobin may be found in the cavities of the capsules. While, however, we have evidence that the epithelium of the capsule has a certain selective power and is the special seat of transmission of particular, especially abnormal, urinary constituents, yet on the whole the glomeruli provide a merely physical apparatus. Through them most of the bulk of the urine passes out, and, flushing the more active portions of the tubules on its course to the pelvis of the kidney, picks up from them the more specific urinary constituents.

Urea is the most important and most abundant of the characteristic ingredients of urine, and it has a very marked influence on kidney activity, the injection of some of it into blood causing a greatly increased secretion of urine, in which the injected urea is quickly passed out. Judging from experiments on amphibia, urea is not excreted or at any rate not chiefly excreted by the glomeruli. On tying the renal arteries of one of these animals urinary secretion ceases, there being then no blood-pressure in the glomeruli to cause the transudation of liquid; but if some urea be now injected into the blood the epithelial cells of other parts of the tubules are stimulated to secrete, and urine rich in urea is formed; but in these circumstances it cannot come from the Malpighian bodies. It would seem then that urea is a special stimulant to some cells of the tubules, and that an excess of it in the blood can stir them up to its elimination along

with some water, quite independently of any formation of transudation urine. In mammalia we cannot separate the glomerular secretion from the tubular as in amphibia; and the diuresis which administration of urea causes in them is in part due to increased glomerular activity, as urea dilates the kidney vessels and causes more blood flow through the glomeruli, which causes the transudation of more water through them; but the simultaneous increase of urea is almost certainly due to special activity of the other parts of the tubules.

The proteids and albuminoids of food may while within the organism have been built up into tissue or may have remained in solution in the liquids; but in either case they are sooner or later broken up and oxidized, the main final products being carbon dioxide, water, and urea. But this breaking down may and does occur in many stages and by different modes in the various tissues; and there is no doubt that most of the intermediate processes in the chemical degradation of albuminous compounds take place outside the kidneys. It was, however, at one time believed that the urea itself was a kidney product : that the penultimate nitrogenous products of proteid degradation were brought to the kidneys, and that there the final formation of urea took place. But if this were so there could not be less urea in the blood leaving the kidneys by their veins than in that brought to them by the renal arteries; yet such is the case. And further, if urea be made in the kidneys it ought not to accumulate in the blood of animals from whom both kidneys have been removed, as it is now known to do, though not the immediate cause of the symptoms of so-called *uræmic poisoning* seen in persons with extensive kidney disease. So far, then, as urea is concerned the cells of the kidney tubules are not its producers; they have a special affinity for it and pick it up from the lymph of the kidney, which in turn gets it from the blood. The cells then pass it on with some water, and no doubt other things, into the tubules which they line. That it is the epithelial cells of the contorted portions of the tubules which especially exercise this selective power is, so far as urea is concerned, a presumption based on their histological characters, but there is evidence that these cells have a special selective power for some other substances circulating in the blood.

A blue substance known as sodium sulphindogate•after injection, in solution, into a vein of an animal is excreted in the bile and urine. If the animal be killed during the excretion no traces of this body can under normal circumstances be detected in any special part of the kidney; it is in fact washed away by the urine as fast as the cells pick it up and pass it into the tubuli. But if the blood-pressure of the animal be made so low (as by cutting the main vaso-constrictor nerves) as to bring the renal secretion to a stand, and the animal be killed some time after injection of the indigotate, the glomeruli and most of the tubules are found free of the blue, which lies only in the contorted portions, just where the cells which gathered it from the circulating liquid had passed it out.

Though the renal epithelium does not make urea it has constructive powers as regards some other urinary constituents. As already stated, benzoic acid taken with the food leaves the Body as hippuric acid, having been combined with glycin. If blood containing benzoic acid and glycin be artificially circulated through a perfectly fresh still living kidney, the renal vein blood will contain hippuric acid. Even if no glycin be provided in the blood injected through the renal artery the returning blood will still yield hippuric acid. So living kidney cells can not only perform the synthesis, with dehydration, necessary to form hippuric acid, but can also form and supply the required glycin. The process is closely dependent on the vitality of the cells; the experiment fails if the organ be not perfectly fresh and uninjured, and if the blood supplied be not properly arterialized.

The Influence of Renal Blood-flow on the Amount of Urine Secreted. From the structure of the glomeruli and the fact that most of the water of the urine is derived from them it is *a priori* probable that anything tending to increase the pressure of blood in them will increase the bulk of urine secreted, and anything diminishing that pressure decrease the urine. This is confirmed by experiment. The kidney is supplied with both vaso-constrictor and vaso-dilator nerves which reach it mainly through the solar plexus, though both sets come ultimately from the spinal cord. When the spinal cord is cut in the neck region of a dog the kidney vessels as well as those of the rest of its body dilate and blood-pressure everywhere is very low. Under these

circumstånces the secretion of urine is suppressed. If the lower end of the cut cord be stimulated the vessels all over the body of the animal contract, and blood-pressure everywhere becomes very high. But the kidney vessels being constricted with the rest allow very little blood to enter the glomeruli in spite of the high aortic pressure, and little or no urine is secreted. If, however, the vasoconstrictor nerves of the kidney be cut before the stimulation of the cord, we get a dilatation of the kidney vessels with a constriction of vessels elsewhere, and abundant blood flows through the glomeruli under high pressure : the whole kidney swells and abundant urine is formed. When the skin vessels contract on exposure to cold, more blood flows through internal organs, the kidneys included, and the blood-pressure in these is if anything increased, the expansion of internal arteries not at the most more than counterbalancing the constriction of the cutaneous. Hence the greater secretion of urine in cold weather. Injection of a little water into a vein of an animal causes a very transient constriction of the kidney vessels followed by a dilatation; and general blood-pressure not being at the same time lowered, pressure in the renal glomeruli is high and the secretion of urine increased. Urea introduced into the blood acts in a similar way, but more markedly, so that this substance causes diuresis not merely, as we have seen, by stimulating the cells of the tubuli, but also by exciting the vaso-dilator nerves of the glomerular arteries. Solution of sodium acetate or even of common salt injected into the veins causes very marked local vascular dilatation in the kidney, and hence great flow through the organ under high pressure and a marked increase in the quantity of urine excreted. Even if the nerves going to the kidney be first cut, the above results follow, these salts appearing to act directly on a local renal vaso-dilator mechanism. They may of course also, like urea, directly stimulate the cells of the contorted tubules, but this is not proved. The increased secretion of urine after drinking much water is probably produced by the dilution of the blood by the liquid absorbed by the alimentary canal, essentially in the same manner as the extra secretion caused by direct injection of water into the blood-vessels. That the central nervous system may influence the renal secretion is well known, fear, for example, stimulating it. Probably

such influence is mainly due to vaso-motor changes—either paralysis of the renal vaso-constrictor nerves or stimulation of the vaso-dilator. Such changes would account for the phenomenon, and there is no evidence of the existence of true secretory nerves acting directly on the cells of the organ as certain fibres of the chorda tympani (Chap. XIX) do on the cells of the submaxillary gland.

The **Skin,** which covers the whole exterior of the Body, consists everywhere of two distinct layers ; an outer, the *cuticle* or *epidermis,* and a deeper, the *dermis, cutis vera,* or *corium.* A blister is due to the accumulation of liquid between these two layers. The *hairs* and *nails* are excessively developed parts of the epidermis.

The **Epidermis,** Fig. 135, consists of cells, arranged in many layers, and united by a small amount of cementing substance. The deepest layer, *d,* is composed of elongated or columnar cells, set on with their long axes perpendicular to the corium beneath. To it succeed several layers of roundish cells, *b,* the deepest of which, *prickle cells,* are covered by minute processes (not indicated in the figure) which do not interlock but join end to end so as to leave narrow spaces between the cells ; in more external layers the cells become more and more flattened in a plane parallel to the surface. The outermost epidermic stratum is composed of many layers of extremely flattened cells from which the nuclei (conspicuous in the deeper layers) have disappeared. These superficial cells are dead and are constantly being shed from the surface of the Body, while their place is taken by new cells, formed in the deeper layers, and pushed up to the surface and flattened in their progress. The change in the form of the cells as they travel outwards is accompanied by chemical changes, and they finally constitute a semitransparent dry *horny stratum, a,* distinct from the deeper, more opaque and softer *Malpighian* or *mucous layer, b* and *d,* of the epidermis. The cells of this latter, in spite of their name, are not muceginous; they are soluble in acetic acid ; those of the horny stratum not.

The rolls of material which are peeled off the skin in the "shampooing" of the Turkish bath, or by rubbing with a rough towel after an ordinary warm bath, are the dead outer scales of the horny stratum of the epidermis.

In dark races the color of the skin depends mainly on minute *pigment granules* lying in the cells of the deeper part of the Malpighian layer.

No blood or lymphatic vessels enter the epidermis, which is entirely nourished by matters derived from the subjacent

Fig. 136.—A section through the epidermis, somewhat diagrammatic, highly magnified. Below is seen a papilla of the dermis, with its artery, *f*, and veins, *gg*; *a*, the horny layer of the epidermis ; *b*, the rete mucosum or Malpighian layer; *d*, the layer of columnar epidermic cells in immediate contact with the dermis ; *h*, the duct of a sweat-gland.

corium. Fine nerve-fibres run into it and end there among the cells.

The Corium, Cutis Vera, or True Skin, Fig. 136, consists fundamentally of a close feltwork of elastic and white fibrous tissue, which, becoming wider meshed below, passes gradually into the *subcutaneous areolar tissue* (Chap. VIII) which attaches the skin loosely to parts beneath. In tanning it is the

cutis vera which is turned into leather, its white fibrous tissue
forming an insoluble and tough compound with the tannin
of the oak-bark employed. Wherever there are hairs, bun-
dles of plain muscular tissue are found in the corium ; it
contains also a close capillary network and numerous lym-
phatics and nerves. In shaving, so long as the razor keeps
in the epidermis there is no bleeding; but a deeper cut shows
at once the vascularity of the true skin.

The outer surface of the corium is almost everywhere
raised into minute elevations, called the *papillæ*, on which

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Fig. 136.—A section through the skin and subcutaneous areolar tissue. h,
horny stratum, and m, deeper more opaque layer of the epidermis ; d, dermis
passing below into sc, loose areolar tissue, with fat, f, in its meshes ; above, dermic
papillæ are seen, projecting into the epidermis which is moulded on them. a,
opening of a sweat-gland , gl, the gland itself.

the epidermis is moulded, so that its deep side presents pits
corresponding to the projections of the dermis. In Fig. 135
is shown a papilla of the *corium* containing a knot of blood-
vessels, supplied by the small artery. *f*, and having the blood
carried off from them by the two little veins, *g g*. Other
papillæ contain no capillary loops but special organs connected
with nerve-fibres, and supposed to be concerned in the sense

of touch (Chap. XXXV). On the palmar surface of the hand the dermic papillæ are especially well developed (as they are in most parts where the sense of touch is acute) and are frequently *compound*, or branched at the tip. On the front of the hand, they are arranged in rows; the epidermis fills up the hollows between the papillæ of the same row, but dips down between adjacent rows, and thus are produced the finer ridges seen on the palms. In many places the corium is also furrowed, as opposite the finger-joints and on the palm. Elsewhere such furrows are less marked, but they exist over the whole skin. The epidermis closely follows all the hollows, and thus they are made visible from the surface. The wrinkles of old persons are due to the absorption of subcutaneous fat and of other soft parts beneath the skin, which, not shrinking itself at the same rate, is thrown into folds.

Hairs. Each hair is a long filament of epidermis developed on the top of a special dermic papilla, seated at the bottom of a depression reaching down from the skin into the tissue beneath, and called the *hair-follicle*. The portion of a hair buried in the skin is called its *root;* this is succeeded by a *stem* which, in an uncut hair, tapers off to a *point.* The stem is covered by a single layer of overlapping scales forming the *hair-cuticle;* the projecting edges of these scales are directed towards the top of the hair. Beneath the hair-cuticle comes the *cortex*, made up of greatly elongated cells united to form fibres; and in the centre of the shaft there is found, in many hairs, a *medulla*, made up of more or less rounded cells. The color of hair is mainly dependent upon pigment granules lying between the fibres of the cortex. All hairs contain some air cavities, especially in the medulla. They are very abundant in white hairs and cause the whiteness by reflecting all the incident light, just as a liquid beaten into fine foam looks white because of the light reflected from the walls of all the little air cavities in it. In dark hairs the air cavities are few.

The hair-follicle (Fig. 137) is a narrow pit of the dermis, projecting down into the subcutaneous areolar tissue, and lined by an involution of the epidermis. At the bottom of the follicle is a papilla, and the epidermis, turning up over this, becomes continuous with the hair. On the papilla epidermic cells multiply rapidly so long as the hair is growing, and the whole hair is there made up of roundish cells. As

these get pushed up by fresh ones formed beneath them, the outermost layer become flattened and form the hair cuticle; several succeeding layers elongate and form the cortex; while, in hairs with a medulla, the middle cells retain pretty much their original form and size. Pulled apart by the elongating cortical cells, these central ones then form the medulla with its air cavities. The innermost layer of the epidermis lining the follicle, has its cells projecting, with

FIG. 137.—Parts of two hairs imbedded in their follicles. *a*, the skin, which is seen to dip down and line the follicle; *b*, the subcutaneous tissue. *c*, the muscles of the hair-follicle, which by their contraction can erect the hair; *o*, sebaceous gland.

overlapping edges turned downwards. Accordingly these interlock with the upward directed edges of the cells of the hair-cuticle; consequently when a hair is pulled out the epidermic lining of the follicle is usually brought with it. So long as the dermic papilla is left intact a new hair will be formed, but not otherwise. Slender bundles of unstriped muscle (*c*, Fig. 137) run from the dermis to the side of the hair-follicles. The latter are in most regions obliquely implanted in the skin so that the hairs lie down on the surface of the Body, and the muscles are so fixed that when they shorten, they erect the hair and cause it to bristle, as may be seen in an angry cat, or sometimes in a greatly terrified man. Opening into each hair-follicle are usually a couple of sebaceous or oil glands. Hairs are found all over the skin except on the palms of the hands and the soles of the feet; the back of the last phalanx of the fingers and toes, the upper eyelids, and one or two other regions.

Nails. Each nail is a part of the epidermis, with its horny stratum greatly developed. The back part of the nail fits behind into a furrow of the dermis and is called its *root*. The visible part consists of a *body*. fixed to the dermis beneath (which forms the *bed of the nail*), and of a *free edge*. Near the root is a little area whiter than the rest of the nail and called the *lunula*. The whiteness is due in part to the nail being really more opaque there. and partly to the fact that its bed, which seen through the nail causes its pink color, is in this region less vascular.

The portion of the corium on which the nail is formed is called its *matrix*. Posteriorly this forms a furrow lodging the root, and it is by new cells added on there that the nail grows in length. The part of the matrix lying beneath the body of the nail, and called its *bed*, is highly vascular and raised up into papillæ which, except in the region of the *lunula*, are arranged in longitudinal rows, slightly diverging as they run towards the tip of the finger or toe. It is by new cells formed on its bed and added to its under surface that the nail grows in thickness, as it is pushed forward by the new growth in length at its root. The free end of a nail is therefore its thickest part. If a nail is "cast" in consequence of an injury, or torn off, a new one is produced, provided the matrix is left.

The Glands of the Skin are of two kinds, the *sudoriparous* or *sweat glands*, and the *sebaceous* or *oil glands*. The former belong to the tubular, the latter to the racemose type. The *sweat-glands*, Fig. 138, lie in the subcutaneous tissue, where they form little globular masses composed of a coiled tube. From the coil a duct (sometimes double) leads to the surface, being usually spirally twisted as it passes through the epidermis. The secreting part of the gland consists of a connective-tissue tube, continuous along the duct with the dermis; within this is a basement membrane; and the final secretory lining consists of several layers of gland-cells. A close capillary network intertwines with the coils of the gland. Sweat-glands are found on all regions of the skin, but more closely set in some places, as the palms of the hands and on the brow, than elsewhere: there are altogether about two and a half millions of them opening on the surface of the Body.

The *sebaceous glands* nearly always open into hair-follicles, and are found wherever there are hairs. Each consists of a duct opening near the mouth of a hair-follicle and branching at its other end: the final branches lead into globular secreting saccules,

Fig. 138.—A sweat gland. *d* horny layer of cuticle; *c,* Malpighian layer; *b,* dermis. The coils of the gland proper, imbedded in the subcutaneous fat, are seen below the dermis.

which, like the ducts, are lined with epithelium. In the

saccules the substance of the cells becomes charged with oil-drops, the protoplasm disappearing; and finally the whole cell falls to pieces, its detritus constituting the secretion. New cells are, meanwhile, formed to take the place of those destroyed. Usually two glands are connected with each hair-follicle, but there may be three or only one. A pair of seba-ceous glands are represented on the sides of each of the hair-follicles in Fig. 137.

The Skin Secretions. The skin besides forming a pro-tective covering and serving as a sense-organ (Chap. XXXV) also plays an important part in regulating the temperature of the Body, and, as an excretory organ, in carrying off certain waste products.

The sweat poured out by the sudoriparous glands is a transparent colorless liquid, with a peculiar odor, varying in different races and, in the same individual, in different regions of the Body. Its quantity in twenty-four hours is subject to great variations, but usually lies between 700 and 2000 grams (10,850 and 31,000 grains). The amount is influenced mainly by the surrounding temperature, being greater when this is high; but it is also increased by other things tending to raise the temperature of the Body, as muscular exercise. The sweat may or may not evaporate as fast as it is secreted; in the former case it is known as *insensible,* in the latter as *sensible perspiration.* By far the most passes off in the in-sensible form, drops of sweat only accumulating when the secretion is very profuse, or the surrounding atmosphere so humid that it does not readily take up more moisture. The perspiration is acid, and in 1000 parts contains 990 of water to 10 of solids. Among the latter are found urea (1.5 in 1000), fatty acids, sodium chloride, and other salts. In dis-eased conditions of the kidneys the urea may be greatly increased, the skin supplementing to a certain extent defi-ciencies of those organs.

The Nervous and Circulatory Factors in the Sweat Secretion. It used to be believed that an increased flow of blood through the skin would suffice of itself to cause in-creased perspiration; but against this view are the facts that, in terror for example, there may be profuse sweating with a cold pallid skin; and that in many febrile states the skin may be hot and its vessels full of blood, and yet there may be no sweating.

Direct experiment shows that the secretory activity of the sweat-glands is under immediate control of nerve-fibres, and is only indirectly dependent on the blood-supply in their neighborhood. Stimulating the sciatic nerve of the freshly amputated leg of a cat will cause the balls of its feet to sweat, although there is no blood flowing through the limb. On the other hand, if the sciatic nerve be cut so as to paralyze it, in a living animal, the skin arteries dilate and the foot gets more blood and becomes warmer; but it does not sweat. The *sweat-fibres* originate in certain *sweat-centres* in the spinal cord, which may either be directly excited by blood of a higher temperature than usual flowing through them or, reflexly, by warmth acting on the exterior of the Body and stimulating the sensory nerves there. Both of these agencies commonly also excite the vaso-dilator nerves of the sweating part, and so the increased blood-supply goes along with the secretion; but the two phenomena are fundamentally independent.

The Sebaceous Secretion. This is oily, semifluid, and of a special odor. It contains about 50 per cent of fats (olein and palmatin). It lubricates the hairs and usually renders them glossy, even in persons who use none of the various compounds sold as " hair-oil." No doubt, too, it gets spread more or less over the skin and makes the cuticle less permeable by water. Water poured on a healthy skin does not wet it readily but runs off it, as " off a duck's back " though to a less marked degree.

Hygiene of the Skin. The sebaceous secretion, and the solid residue left by evaporating. sweat, constantly form a solid film over the skin, which must tend to choke the mouths of the sweat-glands (the so-called " pores " of the skin) and impede their activity. Hence the value to health of keeping the skin clean: a daily bath should be taken by every one. Women cannot well wash their hair daily as it takes so long to dry, but a man should immerse his head when he takes his bath. As a general rule, soap should only be used occasionally; it is quite unnecessary for cleanliness, except on exposed parts of the Body, if frequent bathing be a habit and the skin be well rubbed afterwards until dry. Soap nearly always contains an excess of alkali which in itself injures some skins, and, besides, is apt to combine chemically with the sebaceous secretion and carry it too freely away.

Persons whose skin will not stand soap can find a good substitute, for washing the hands and face, in a little cornmeal. No doubt many folk go about in very good health with very little washing; contact with the clothes and other external objects keeps its excretions from accumulating on the skin to any very great extent. But apart from the duty of personal cleanliness imposed on man as a social animal in daily intercourse with others, the mere fact that the healthy Body can manage to get along under unfavorable conditions is no reason for exposing it to them. A clogged skin throws more work than their fair share on the lungs and kidneys, and the evil consequences may be experienced any day when something else puts another extra strain on them.

Animals, a considerable portion of whose skin has been varnished, die within a few hours. This used to be thought due to poisoning by retained ingredients of the sweat. But the main cause of death seems to be an excessive radiation of heat from the surface of the body, dependent mainly on dilatation of the cutaneous vessels caused by the varnish, though possibly the retention of some poisonous substance usually excreted by the skin may have an influence. The bodily temperature falls in consequence of the great loss of heat until it reaches the fatal point, about 20° C. (68° F.) for rabbits. If the animal be packed in raw cotton or kept in an atmosphere at a temperature of 30° C. (86° F.) it does not die as a consequence of the varnishing, or at least not nearly so soon as it would otherwise die.

Bathing. The general subject of bathing may be considered here. One object of it is that above mentioned—to cleanse the skin; but it is also useful to strengthen and invigorate the whole frame. For strong healthy persons a cold bath is the best, except in extremely severe weather, when the temperature of the water should be raised to 15° C. (about 60° F.), at which it still feels quite cold to the surface. The first effect of a cold bath is to contract all the skin-vessels and make the surface pallid. This is soon followed by a reaction, in which the skin becomes red and congested, and a glow of warmth is felt in it. The proper time to come out is while this reaction lasts, and after emersion it should be promoted by a good rub. If the stay in the cold water be too prolonged the state of reaction passes off, the skin becomes cold and pale and the person feels chilly, uncomforta-

ble, and depressed all day. Then bathing is injurious instead of beneficial; it lowers instead of stimulating the activities of the Body. How long a stay in the cold water may be made with benefit depends greatly on the individual: a vigorous man can bear and set up a healthy reaction after much longer immersion than a feeble one; moreover, being used to cold bathing renders a longer stay safe, and, of course, the temperature of the water has a great influence: water called " cold " may vary within very wide limits of temperature, as indicated by the thermometer; and the colder it is the shorter is the time which it is wise to remain in it. Persons who in the comparatively warm water of Narragansett during the summer months stay with benefit and pleasure in the sea, have to content themselves with a single plunge on parts of the coast where the water is colder. The nature of the water has some influence; the salts contained in sea-water stimulate the skin-nerves and promote the afterglow. Many persons who cannot stand a simple cold fresh-water bath take one with benefit when some salines are previously dissolved in the water. The best for this purpose are probably those sold in the shops under the name of " sea-salts."

It is perfectly safe to bathe when warm, provided the skin is not perspiring profusely, the notion commonly prevalent to the contrary notwithstanding. On the other hand, no one should enter a cold bath when feeling chilly, or in a depressed vital condition. It is not wise to take a bath immediately after a meal, since the afterglow tends to draw away too much blood from the digestive organs, which are then actively at work. The best time for a long bath is about three hours after breakfast; but for an ordinary daily dip, lasting but a short time, there is no better period than on rising and while still warm from bed.

The shower-bath abstracts less heat from the skin than an ordinary cold bath and, at the same time, gives it a greater stimulus: hence it has certain advantages.

Persons in feeble health may diminish the shock to the system by raising the temperature of the water they bathe in up to any point at which it still feels cool to the skin. Bathing in water which feels hot is not advisable: it tends generally to diminish the vital activity of the Body. Hence warm baths should only be taken occasionally and for special purposes, other than mere luxury.

CHAPTER XXIX.

NUTRITION.

The Problems of Animal Nutrition. We have in preceding chapters traced certain materials, consisting of foods more or less changed by digestion, into the Body from the alimentary canal, and oxygen into it from the lungs. We have also detected the elements thus taken into the Body in their passage out of it again by lungs, kidneys, and skin; and found that for the most part their chemical state was different from that in which they entered; the difference being expressible in general terms by saying that more oxidized forms of matter leave the Body than go into it. We have now to consider what happens to each food during the journey through the Body: is it changed at all? is it oxidized? if so where? what products does its oxidation give rise to? Is the oxidation direct and complete at once, or does it occur in successive steps? Has the food been used first to make part of a living tissue and is that then oxidized; or has it been oxidized without forming part of a living tissue? if so, where? in the blood stream, or outside of it? Finally, if the chemical changes undergone in the Body are such as to liberate energy, how has this energy been utilized? to maintain the temperature of the Body or to give rise to muscular work, or for other purposes? This is a long string of questions, the answers to many of which Physiology has still to seek.

The Seat of the Oxidations of the Body. According to elder views oxidation mainly took place in the blood while flowing through the lungs. Those organs were considered a sort of furnace in which heat was liberated by blood oxidation, and then distributed by the circulation. But if this were so the lungs ought to be the hottest parts of the Body, and the blood leaving them by the pulmonary veins much hotter than that brought to them by the pulmonary artery after it had been cooled by warming all the tissues; and neither of these

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things is true. A small amount of heat is liberated when hæmoglobin combines with oxygen in the pulmonary capillaries, but the affinities thus satisfied are so feeble that the energy liberated is trivial in amount when compared with that set free when this oxygen subsequently forms stabler compounds elsewhere. There is good reason to believe that hardly any of this latter class of oxidations occurs in the living circulating blood at all; its cells do, no doubt, use up some oxygen and set free some carbon dioxide; but not enough to be detected by ordinary methods of analysis. The percentage of oxygen liberated in a vacuum by two specimens of the blood of an animal, taken one from an artery near the heart, and the other from a distant one, are practically the same; showing that during the time occupied in flowing two or three feet through an artery the blood uses up no appreciable quantity of its own oxygen; while in its brief capillary transit it almost suddenly loses so much oxygen as to become venous. The difference is explained by the fact that the blood gives off oxygen gas through the thin capillary walls to the surrounding tissues; and in the latter the oxidation takes place. As we have already seen, a freshly excised muscle deprived of blood can still be made to contract; and for some considerable time if it be the muscle of a cold-blooded animal. During its contraction it evolves large amounts of carbon dioxide, although the resting fresh muscle contains hardly any of that gas. Here we have direct evidence of oxidation taking place in a living tissue and in connection with its functional activity; and what is true of a muscle is probably true of all tissues: the oxidations which supply them with energy take place within the living cells themselves. The statement frequently made that the oxygen in the circulating blood exists as ozone, rests on no sufficient basis; decomposing hæmoglobin does ozonize some oxygen when exposed to the air, but there is no ozone in fresh blood. Experiments made by adding various combustible substances, as sugar, to newly drawn blood, also fail to prove the occurrence of any oxidation of such bodies in that liquid.

Tissue-Building and Energy-Yielding Foods. The Human Body, like that of other animals, is, on the whole, chemically destructive; it takes in highly complex substances as food, and eliminates their elements in much simpler compounds, which can again be built up to their original

condition by plants. Nevertheless the Body has certain con-
structive powers: it, at least, builds up protoplasm from
proteids and other substances received from the exterior;
and there is reason to believe it does a good deal more of the
same kind of work, though never an amount equalling its
chemical destructions. Given one single proteid in its food,
say egg albumen, the Body can do very well; making serum
albumen and paraglobulin out of it for the blood, myosinogen
for the muscles, and so on: in such cases the original proteid
must have been taken more or less to pieces, remodelled, and
built up again by the living tissues; and it is extremely
doubtful if anything different occurs in other cases, when
the proteid eaten happens to be one found in the Body. In
fact, during digestion the proteids are broken down some-
what and turned into peptones; in this state they are absorbed
and must somewhere again be built up into the proteids of
the tissues.

The constructive powers of the Body used to be rather
too much ignored. Foods were divided into *assimilable* and
combustible, the former serving directly to renew the organs
or tissues as they were used up, or to supply materials for
growth; these were mainly proteids and fats; no special
chemical synthesis was thus supposed to take place, the living
cells being nourished by the reception from outside of mole-
cules similar to those they had lost. Fat-cells, it was sup-
posed, grew by picking up fatty molecules like their contents,
received from the food; and albumen-rich tissues by the re-
ception of ready-made proteid molecules, needing no further
manufacture in the cell. The combustible foods, on the other
hand, were the carbohydrates and some fat: the carbohy-
drates, according to the hypothesis, were incapable of being
made into parts of a living tissue, and were merely oxidized
in order to maintain the bodily warmth. It having been
proved, however, that more fat might accumulate in the body
of an animal than was taken in its food, this excess was ac-
counted for by supposing it was due to excess of com-
bustible foods, converted into fats and stored away as oil-
droplets in various cells; but not actually built up into true
living adipose tissue. Liebig, somewhat similarly, classed all
foods into *plastic,* concerned in making new tissue, and
respiratory, directly oxidized before they ever constituted
part of a tissue. The plastic foods were the proteids, but

these also indirectly gave rise to the energy expended in muscular work, and to some heat: the proteid muscular fibre being broken first into a highly nitrogenous part (urea, or some body well on the road to become urea) and a non-nitrogenized richly hydrocarbonous part; and this latter was then oxidized and gave rise to heat. Several facts may be urged against this view: (1) Men in tropical climates live mainly on non-proteid foods, yet their chief needs are not heat production, but tissue formation and muscular work: according to Liebig's view their diet should be mainly nitrogenous. (2) Carnivorous animals live on a diet very rich in proteids, nevertheless develop plenty of animal heat, and that without doing the excessive muscular work which, on Liebig's theory, must first be gone through in order to break up the proteids, with the production of a non-azotized part which could then be oxidized for heat-production. (3) Great muscular work can be done on a diet poor in proteids; beasts of burden are for the most part herbivorous. (4) Further, we know exactly how much energy can be liberated by the oxidation of proteids to that stage which occurs in the Body; and it is possible to estimate with considerable accuracy the amount of urea and uric acid excreted in a given time; from their sum the amount of proteid oxidized and the amount of energy liberated in that oxidation can be calculated; if this be done it is found that, nearly always, the muscular work done during the same period represents far more energy expended than could be yielded by the proteids broken down.

The Source of the Energy Expended in Muscular Work. This important question, which was postponed in the chapters dealing with the physiology of the muscular tissues, needs now consideration. It may be put thus : Does a muscle-fibre work by the oxidation of its proteids, *i.e.* by breaking them down into compounds which are then removed from it and conveyed out of the Body? or does it work by the energy liberated by the oxidation of carbon and hydrogen compounds only? The problem may be attacked in two ways: first, by examining the excretions of a man, or other animal, during work and rest; second, by examining directly the chemical changes produced in a muscle when it contracts. Both methods point to the same conclusion, viz., that proteid oxidation is not the source of the mechanical energy expended by the Body.

One gram (15.5 grains) of pure albumen when completely burnt liberates, as heat, an amount of energy equal to 2117 kilogrammeters (15,270 foot-pounds). But in the Body proteids are not fully oxidized ; part of their carbon is, to form carbon dioxide, and part of the hydrogen, to form water; but some carbon and hydrogen pass out, combined with nitrogen and oxygen, in the incompletely oxidized state of urea. Therefore all of the energy theoretically obtainable is not derived from proteids in the Body: from the above full amount for each gram of proteid we must take the quantity carried off in the urea, which will be the amount liberated when that urea is completely oxidized. Each gram (15.5 grains) of proteid oxidized in the Body gives $\frac{1}{3}$ of a gram (5.14 grains) of urea ; since one gram of urea liberates, on oxidation, energy amounting to 934 kilogrammeters (6740 foot-pounds), each gram of proteid oxidized, so far as is possible in the Body, will yield during the process $2117 - \frac{934}{3} = 1805.7$ kilogrammeters (13,037 foot-pounds) of energy. Knowing that urea carries off practically all the nitrogen of proteids broken up in the Body, and contains 46.6 per cent of nitrogen, while proteids contain 16 per cent, it is easy to find that each gram of urea represents the decomposition of about 2.80 grams of proteid and, therefore, the liberation of 5060.00 kilogrammeters (36,533.0 foot-pounds) of energy. If, therefore, we know how much urea a man excretes during a given time, and how much mechanical work he does during the same time, we can readily discover if the latter could possibly have been done by the energy set free by proteid decomposition. Let us take a special case. Fick and Wislecenus, two German observers, climbed the Faulhorn mountain, which is 1956 meters (about 6415 feet) high. Fick weighed 66 kilograms and, therefore, in lifting his Body alone, did during the ascent 129,096 kilogrammeters (932,073 foot-pounds) of work. Wislecenus, who weighed 76 kilograms, did similarly 148,656 kilogrammeters (1,073,296 foot-pounds) of work. But during the ascent, and for five hours afterwards, Fick secreted urine containing urea answering only to 37.17 grams of proteid, and Wislecenus urea answering to 37 grams. Since each gram of proteid broken up in the Body liberates 1805.7 kilogrammeters (13,037 foot-pounds) of energy, the amount that Fick could possibly have obtained from such a source is $1805.7 \times 37.17 = 67,117$ kilogrammeters (484,584

foot-pounds), and Wislecenus 1805.7 × 37 = 66,810 kilo-grammeters. If to the muscular work done in actually rais-ing their bodies, we add that done simultaneously by the heart and the respiratory muscles, and in such movements of the limbs as were not actually concerned in lifting the weight, we should have, at least, to double the above total muscular work done ; and the amount of energy liberated meanwhile by proteid oxidation, becomes utterly inadequate for its execution. It is thus clear that muscular work is not wholly done at the expense of the oxidation of muscle pro-teid; and it is very probable that none is so done under ordi-nary circumstances, for the urea excretion during rest is about as great as that during work, if the diet remain the same: if the work be very severe, as in long-distance walking-matches, the urea quantity is sometimes temporarily raised, but this increase, which no doubt represents an abnormal wear and tear of muscle-fibre, is probably independent of the liberation of energy in the form in which a muscle can use it, more likely taking the form of heat ; and is, moreover, com-pensated for afterwards by a diminished urea excretion. Thus, hourly, before the ascent Fick and Wislecenus each excreted on the average about 4 grams (62 grains) of urea; during the ascent between 7 and 8 grams (108–124 grains); but during the subsequent 16 hours, when any urea formed in the work would certainly have reached the urine, only an average of about 3 grams (46.5 grains) per hour.

It may still be objected, however, that a good deal of the muscle work may be done by the energy of oxidized muscle proteid; that the amount of this oxidation occurring in a muscle during rest or ordinary work is pretty constant and simply takes different forms in the two cases, much as a steam-engine with its furnace in full blast will burn as much coal when resting as when working, but in the former case lose all the generated energy in the form of heat, and in the latter partly as mechanical work. Thus the smallness of in-crease in urea excretion as a consequence of muscular activity could be explained, while still a good deal of utilizable energy might come from proteid degradation. But if this were so, then the working Body should eliminate no more carbon dioxide than the resting; the amount of chemical changes in its muscles being by hypothesis the same, the carbon dioxide eliminated should not be increased. Experiment, however,

shows that it is, and that to a very large extent, even when the work done is quite moderate and falls within the limits which could be performed by the normal proteid degradation of the Body. Quite easy muscular work doubles the carbon dioxide excreted in twenty-four hours, and in a short period of very hard work it may rise to five times the amount eliminated during rest. Since the urea is not increased, or but slightly increased, at the same time, this carbon dioxide cannot be due to increased proteid metamorphosis; and it therefore indicates that a muscle works by the oxidation of carbonaceous non-nitrogenous compounds. Since all the carbon compounds oxidized in the Body contain hydrogen this element is also no doubt oxidized during muscular work; but the estimation of the amount so used is difficult and has not been satisfactorily made, because the Body contains so much water ready formed that a large quantity is always ready for increased evaporation from the lungs and skin, whenever the respirations are quickened, as they are by exercise. It, thus, is very difficult to say how much of the extra water eliminated from the Body during work is due merely to this cause and how much to increased hydrogen oxidation.

The conclusion we are led to is, then, that a muscle works by the oxidation mainly. if not entirely, of carbon and hydrogen: and that the proteid constituents of the living muscle substance are essentially the machinery determining in what way the energy shall be spent: they may and do suffer some wear and tear, but this bears no direct proportion to the work done; as a steam-engine may rust, so muscle proteid may and does oxidize, but not to supply the organ with energy for use. This conclusion, arrived at by a study of the excretions of the whole Body, is confirmed by the results obtained by the chemical study of a single muscle. A fresh frog's muscle (which agrees in all essential points with a man's) contains practically no carbon dioxide, yet made to work in a vacuum gives off that gas, and more the more it works Some carbon dioxide is therefore formed in the working muscle. If the muscle, after contracting as long as it can be made to do so, be thrown into death rigor it gives off more carbon dioxide; and if taken perfectly fresh and sent into *rigor mortis* without contracting, it gives off carbon dioxide also, in amount equal to the sum of that

which it would have given off in two stages, if first worked and then sent into rigor. The muscle must, therefore, contain a certain store of a carbon-dioxide-yielding body, and the decomposition of this is associated with the occurrence both of muscular activity and death stiffening. Similar things are true of the acid simultaneously developed; the muscle when it works produces some sarcolactic acid, and when thrown into rigor mortis still more. No increase of urea or kreatin or any similar product of nitrogenous decomposition is found in a worked muscle when compared with a rested one, but the total carbohydrates are rather less in the former. These facts make it clear that muscular work is not done at the expense of proteid oxidation; and we have already seen (Chap. XXVI) that the oxygen a muscle uses in contracting is not taken up by it at the time it is used, since a muscle containing no oxygen will still contract in a vacuum and form carbon dioxide. It is probable that the chemical phenomena occurring in contraction and rigor are essentially the same; the death stiffening results when they occur to an extreme degree. Provisionally one may explain the facts as follows: A muscle in the Body takes up from the blood, oxygen, proteids, and non-nitrogenous (carbohydrate or fatty) substances. These it builds up into a highly complex and very unstable compound, comparable, for example, to nitroglycerine. When the muscle is stimulated this falls down into simpler substances in which stronger affinities are satisfied; among these are carbon dioxide and sarcolactic acid and a proteid (myosinogen). The energy liberated is thus independent of any simultaneous taking up of oxygen; the amount possible depends only on how much of the decomposable body existed in the muscle. Under natural conditions the carbon dioxide is carried off in the blood and perhaps the sarcolactic acid also, the latter to be elsewhere oxidized further to form water and more carbon dioxide. The myosinogen remains in the muscle-fibre and is combined with more oxygen, and with compounds of carbon and hydrogen taken from the blood, and built up into the unstable energy-yielding body again; no increased quantity of nitrogenous material, under ordinary circumstances, leaves the working muscle. If, however, the blood-supply be deficient, myosin forms from myosinogen and clots (Chap. IX) before this restitution takes place, and cannot be directly rebuilt into

living muscle material; in excessive work the same thing partially occurs, decomposition occurring faster than recomposition; clotted myosin is then broken up into simpler bodies as kreatin, and these are somewhere turned into urea and excreted. In *rigor mortis* all the myosinogen passes into clotted myosin and causes the rigidity. A working muscle takes up more oxygen from the blood than a resting one, as is shown by a comparison of the gases of the venous blood of the two; this oxygen assumption is not necessarily proportionate to the carbon-dioxide elimination at the same time; for the latter depends on the breaking down of a material already accumulated in the muscle during rest, and this breaking down may occur faster than the reconstruction. We are thus enabled, also, to understand how, during exercise, the carbon dioxide evolved from the lungs may contain more oxygen than that taken up at the same time; for it is largely oxygen previously stored during rest which then appears in the carbon dioxide of the expired air. The kreatin which can always be found even in muscles suddenly killed after long rest, represents the breaking down of proteid in the chemical processes of the living fibres, in their vital metabolisms, which are not necessarily similar to the special chemical changes associated with a contraction.

Are any Foods Respiratory in Liebig's Sense of the Term? We find, then, that Liebig's classification of foods cannot be accepted in an absolute sense. There is no doubt that the substance broken down in muscular contraction is proper living muscular tissue; and if this (its proteid constituent being retained) be reconstructed from foods containing no nitrogen (whether carbohydrates or fats) then the term *plastic* or tissue-forming cannot be restricted to the proteids of the diet. We must rather conclude that any alimentary principle containing carbon may be used to replace the oxidized carbon, and any containing hydrogen to replace the oxidized hydrogen, of a tissue; and so even non-proteid foods may be plastic. A certain proportion of the foods digested may perhaps be oxidized to yield energy, before they ever form part of a tissue; and so correspond pretty much to Liebig's respiratory foods; but no hard and fast line can be drawn, making all proteid foods plastic and all oxidizable non-proteid foods respiratory.

Luxus Consumption. Not only, as above pointed out,

may non-nitrogenous foods be plastic but, on the other hand, it is certain that if any foods are oxidized at once before being organized into a tissue, proteids are under certain circumstances; namely, when they are contained in excess in a diet. If an animal be starved it is found that its non-nitrogenous tissues go first; an insufficiently fed animal loses its fat first, and if it ultimately dies of starvation is found to have lost 97 per cent of its adipose tissue and only about 30 per cent of its proteid-rich muscular tissue, and almost none of its brain and spinal cord; all of course reckoned by their dry weight. It is thus clear that the proteids of the tissues resist oxidation much better than fat does. But, on the other hand, if a well-fed animal be given a very rich proteid diet all the nitrogen of its food reappears in its urine, and that when it is laying up fat; so that then we get a state of things in which proteids are broken up more easily than fats. This indicates that proteid in the Body may exist under two conditions ; one, when it forms part of a living tissue and is protected to a great extent from oxidation, and another, in which it is oxidized with readiness and is presumably in a different condition from the first, being not yet built up into part of a living cell. The use of proteids for direct oxidation is known as *luxus consumption ;* how far it occurs under ordinary circumstances will be considered presently. The main point now to be borne in mind is that while all organic non-nitrogenous foods cannot be called *respiratory,* neither can proteids under all circumstances be called *plastic,* in Liebig's sense.

The Antecedents of Urea. In the long-run the progenitors of the urea excreted from the Body are the proteids taken in the food; but it remains still to be considered what intermediate steps these take before the excretion of their nitrogen in the urine.

In seeking antecedents of urea one naturally turns first to the muscles, which form by far the largest mass of proteid tissues in the Body. Analysis shows that they always yield kreatin, the quantity of this in muscles being practically unaffected by work, and from 0.2 to 0.3 per cent of the dry weight of the muscle. Since it is readily soluble and dialyzable, and therefore fitted to pass rapidly out of the muscles into the blood stream, it is a fair conclusion that a good deal of it is formed in the muscles daily and carried off from them.

Kreatin, too, exists in the brain, and probably there and elsewhere in the nervous system is produced by chemical degradation of protoplasm; the spleen also contains a good deal of kreatin, and so do many glands. This substance would therefore seem to be constantly produced in considerable quantities by the protoplasmic tissues generally; and since it belongs to a group of nitrogenous compounds which the Body is unable to utilize for reconstruction into proteids, it must be carried off somehow. The urine, however, contains no kreatin and but little of its immediate derivative, kreatinin, and what kreatinin it does contain depends mainly on the feeding, since its amount varies with the diet and it disappears during starvation. Kreatin can readily be chemically broken up with hydration, yielding urea and sarkosin; and sarkosin in turn can be decomposed so as to yield its nitrogen in the form of urea. Hence there are no great chemical difficulties in regarding kreatin as the main immediate source of the urea of normal urine. There are some reasons for thinking that kreatin is not the form of the actual nitrogen waste in living muscle but a post-mortem product from that waste; but that is not of importance in the present connection. Whatever the original form of the waste substance be, if it be not kreatin it is certainly very easily converted into it. The formation of the final product, urea, does not occur in the muscles. They never contain urea; and very little of it, if any, can be extracted from the brain.

Where the kreatin is finally changed into urea is doubtful. We have seen (Chap. XXVIII) that it is not formed in the kidneys but merely separated by them from the blood. A good deal of urea is found in the liver, which suggests some part played by that organ in urea formation. Further, in certain cases of hepatic disease (acute yellow atrophy) in which the liver cells are profoundly changed, the urea of the urine is greatly diminished and a quite different substance, *leucin*, takes its place; and this favors the view that the liver has much to do with the final elaboration of urea. It may also be noted in this connection that, quite apart from kreatin as a source of urea, there may be another in leucin, for leucin is very widely distributed through the Body, and when proteids are decomposed by various chemical methods leucin is very constant among the products. It is therefore a possible form

for the primary nitrogen waste of many tissues. Chemically leucin is an ammonium derivative, being the amide of caproic (a fatty) acid.

While the urea resulting from further changes in the kreatin, leucin, or similar substances formed in the tissues, is a measure of the wear and tear of their protoplasm, part of the urea excreted has probably a different source; being due to the oxidation of proteids as energy liberators or respiratory foods, before they have ever formed a tissue. When abundant proteid food is taken the urea excretion is largely increased and that very rapidly, within a couple of hours for example, and before we can well suppose the proteids eaten to have been built up into tissues, and these in turn broken down; in fact there need be, and usually is, under such circumstances no sign of any special activity of any group of tissues, such as one would expect to see if the urea always came from the breaking down of formed histological elements. This urea is thus indicative of a utilization of proteids for other than plastic purposes; and the same fact is indicated by the storage of carbon and elimination of all the nitrogen of the food when a diet very rich in proteid alimentary principles is taken. This *luxus consumption* may be compared to the paying out of gold by a merchant instead of greenbacks when he has an abundance of both. Only the gold can be used for certain purposes, as settling foreign debts, but any quantity above that needed for such a purpose is harder to store than the paper money, and not so convenient to handle; so it is paid out in preference to the paper money, which is really somewhat less valuable, as available at par only for the settlement of domestic debts. Similarly, only proteids can be used for certain final stages of tissue building, but an excess of them is more difficult to store than fats or carbohydrates, and so is eliminated in preference to them.

In artificial pancreatic digestions, when long carried on, two bodies, called leucin and tyrosin, are produced from proteids. It is found that when leucin is given to an animal in its food, it reappears in the urine as urea; so the Body can turn leucin into that substance. Hence a possible source of some of the *luxus-consumption* urea is leucin produced during intestinal digestion; and this is very likely turned into urea in the liver. Mammalia rapidly die when the liver is

removed, but some birds survive for a time. In them it has been found that the uric acid (which in avian urine has the predominance which urea takes in mammalian) excreted is diminished after extirpation of the liver; and also that leucin which when given to the normal bird reappears in the urine as uric acid, in the bird from which the liver has been removed is excreted unaltered.

Circulating and Fixed Proteid. When an animal is fed on food deficient in proteids, or containing none of them at all, its urea excretion falls very rapidly during the first day or two, but then much more slowly until death: there is thus indicated a double source of urea, a part resulting from tissue wear and tear, and always present; and a part resulting from the breaking down of proteids not built up into tissue, and ceasing when the amount of this proteid in the Body (in the blood for example) falls below a certain limit as a result of the starvation. As the nitrogen-starved Body wastes, its bulk of proteid tissues is slowly reduced and the urea resulting from their degradation diminishes also. How well proteid built up into a tissue resists removal is shown by the facts already mentioned as to the relative losses of the proteid-rich and proteid-poor tissues during starvation.

On the other hand, if an animal be taken while starving and losing weight and have a small amount of flesh given it, it will continue to lose weight, and more urea than before will appear in the urine; increased proteid diet increases the proteid metamorphosis, and the animal still loses, though less rapidly than it did. A little more proteid still increases proteid metamorphosis in its body and its urea elimination, and so on for some time; but each increment of proteid in the food increases the nitrogenous metamorphosis in proportion to itself somewhat less than the preceding one did, until, finally, a point is reached at which the nitrogen egesta and ingesta balance: in a dog this occurs when the animal gets daily $\frac{1}{20}$ its weight of lean meat, along with the necessary water. More flesh if then given is at first stored up and the animal increases in weight; but very soon the greater wear and tear of the larger mass of tissues shows itself as increased urea excretion, and again the egesta and ingesta balance, and the animal comes to a new weight equilibrium at the higher level. More meat now causes a repetition of the phenomenon: at first increase of tissue, and nitrogen storage; and then a

cessation of the gain in weight, and an excretion in twenty-four hours of all the nitrogen taken. And so on, until the animal refuses to eat a larger quantity.

These facts seem, very clearly, to show that proteids cannot be built up quickly into tissues. Meat given to the starving animal has its proteids, at first, used up mainly in *luxus consumption*—while a little is stored as tissue, though at first not enough to counterbalance the daily tissue waste. When a good deal more proteid is given than answers to the nitrogen excretion during starvation, the animal builds up as much into living tissue as it breaks down in the vital processes of these, the rest going in *luxus consumption;* it thus neither gains nor loses. Still more proteid if now given does not all appear in the urine at once; some is used to build up new tissue, but only slowly; then, after some days, the increased metabolism of the increased mass of living tissues balances the excess of nitrogen in the diet, and equilibrium is again attained. But, all through, it seems clear that the tissue formation is slow and gradual; and so it becomes additionally probable that the increased urea excretion soon after a meal is not due to rapidly increased tissue formation and degradation, but to a more direct proteid destruction. The more stable proteid, that which breaks down slowly in starvation and is rebuilt slowly when food is given, has been distinguished as *fixed* or *tissue albumen* from the less stable portion, which from the belief that it mainly exists in the liquids of the Body has been named *circulating albumen* Feeding experiments further show the important fact that the gelatinous or albuminoid foods cannot be converted into fixed proteid; for its formation true albumens are required. The tissues of an animal deprived of all proteid food-stuffs waste, no matter how much albuminoids be given: but given some of the latter the Body can build tissues and maintain their integrity with less true proteid than would otherwise be necessary, so the gelatin-yielding foods are by no means without nutritive value.

The Storage Tissues. Every healthy cell of the Body contains at any moment some little excess of material laid by in itself, above what is required for its immediate necessities. The capacity of contracting, and the concomitant evolution of carbon dioxide, exhibited by an excised muscle in a vacuum, seem to show that even oxygen, of which

warm-blooded animals have but a small reserve, may be stored up in the living tissues in such forms that they can utilize it, even when the air-pump fails to extract any from them. But in addition to the supplies for immediate spending, contained in all the cells, we find special food reserves in the Body, on which any of the tissues can call at need. These, especially the oxygen and proteid reserves, are found for most part in the blood. Special oxygen storage is, however, rendered unnecessary by the fact that the Body can, except under very unusual circumstances, get more from the air at any time, so the quantity of this substance laid by is only small; hence death from asphyxia follows very rapidly when the air-passages are stopped; while, on account of the reserves laid up, death from other forms of starvation is a much slower occurrence. Proteids, also, we have learnt from the study of muscle, are probably but little concerned in energy-production in the tissues. Speaking broadly, the work of the Body is carried on by the oxidation of carbon and hydrogen, and we find in the Body, in correspondence with this fact, two great storehouses of fatty and carbohydrate foods, which serve to supply the materials for the performance of work and the maintenance of the bodily temperature in the intervals between meals, and during longer periods of starvation. One such store, that of carbohydrate material, is found in the liver-cells; the other, or fatty reserve, is laid by in the adipose tissue and to a certain extent in oil droplets found in other cells, and sometimes in blood and lymph. That such substances are true reserves, not for any special local purpose but for the use of the Body generally, is shown by the way they disappear in starvation; the liver reserve in a few days, and the fat somewhat later and more slowly, but very largely before any of the other tissues has been seriously affected. By using these accumulated matters the Body can work and keep warm during several days of more or less deficient feeding; and the fatter an animal is at the beginning of a starvation period the longer will it live; which would not be the case could not its fat be utilized by the working tissues. Hibernating animals prove the same thing; bears, before their winter sle p, are very fat, and at the end of it commonly very thin; while their muscular and nervous systems are not noticeably diminished in mass. During the whole winter, then, the

energy needed to keep the heart and respiratory muscles at work, and to maintain the temperature of the body, must have been obtained from the oxidation of the fat reserve with which the animal started.

Glycogen. The size of the liver was long a stumbling-block to physiologists: it was difficult to understand why so large an organ should be developed for the mere secretion of some bile, a not very important digestive liquid. But even centuries ago some glimmering of the truth was guessed, and the liver was believed to be concerned in the elaboration of *nutritive blood,* which was distinguished from the blood, charged with *vital spirits,* which came from the lungs and the left side of the heart. Harvey's discovery of the real course of the circulation, and Lavoisier's interpretation of the meaning of respiration, upset these crude doctrines; and for long the germ of truth which they contained was lost to view in the glare of the new light. We have now learned, on a new basis of actual experiment, that the liver is very largely concerned in the nutritive processes of the Body: its relation to proteid metabolism and urea formation has already been considered, and we have now to study its activity in regard to the formation, and storage, and transmission of a carbohydrate substance, *glycogen.*

If a liver be cut up two or three hours after removal from the body of a healthy well-fed animal, and thoroughly extracted with water, it will yield much grape-sugar. If, on the other hand, a perfectly fresh liver be heated rapidly to the temperature of boiling water, and be then pounded up and extracted, it will yield a milky solution, containing little grape-sugar, but much *glycogen;* a substance which chemically has the same empirical formula as starch ($C_6H_{10}O_5$), and in other ways is closely allied to that body. The salivary and pancreatic secretions rapidly convert it into the sugar *maltose,* as they do starch. The transformation of glycogen into glucose (grape-sugar) which occurs in the liver after death and probably also during life is then quite different from that brought about by the digestive enzymes; and in fact no enzyme has been extracted from fresh liver. The change is apparently not a fermentative one, but one dependent on some vital metabolic activity of the liver-cells, which activity is greatly accelerated during their period of dying: hence the need of killing them rapidly by boiling, if any considerable amount of

glycogen is to be obtained from the organ. Pure glycogen is a white amorphous inodorous powder, readily soluble in water, forming an opalescent milky solution; insoluble in alcohol, and giving with iodine a red coloration which disappears on heating and reappears on cooling again.

About four per cent of glycogen can be obtained from the liver of a well-nourished animal (dog or rabbit). This for the human liver, which weighs about 1500 grams (53 oz.), would give about 60 grams (2.1 oz.) of glycogen at any one moment. The quantity actually formed daily is, however, much in excess of that, since glycogen is constantly being removed from the liver and carried elsewhere, while a fresh supply is formed in the organ. Its quantity is subject, also, to considerable fluctuations; being greatest about two hours after a good meal, and falling from that time until the next digestion period commences, when it begins to rise until it again attains its maximum. If a warm-blooded animal be starved glycogen disappears from its liver in the course of four or five days. We are, thus, led to believe that glycogen is being constantly used up, and that its maintenance in normal quantity depends on food supply.

The accumulation and disappearance of glycogen can be demonstrated histologically. The liver is essentially a compound tubular gland, but its structure is obscured by the fact that the hepatic cells are very large in proportion to the tubules which they surround, so that these are reduced to mere *ductules,* formed by the apposition of grooves on the adjacent sides of two cells; and by the fact that cells and ductules form an irregular network interlaced with the capillaries of the lobule (Chap. XXII), which capillaries are far larger than the interlobular bile-ducts. When properly prepared hepatic cells, taken from a healthy well-fed animal, are examined, the side of the cell nearest the bile-ductule is seen to be granular, and it also picks up readily most of the ordinary protoplasmic stains. The rest of the cell contains few granules and does not stain with carmine, but it does stain red with iodine. It is in fact mainly filled with glycogen, and if this be dissolved out by digestion with saliva there is left a loose protoplasmic network. If sections from the liver of a starved animal be compared with those from a well-fed, the liver-cells are seen to be considerably smaller, to be granular throughout, and to stain everywhere with carmine

and not at all with iodine: they contain no glycogen and may be compared with the cells of the pancreas in a late stage of digestion (Chap. XIX).

In the liver we have to deal with cells of twofold function; the granular portion of each especially concerned with bile secretion, and the larger portion of the cell with the making of glycogen. In a salivary gland we have cells whose sole apparent function is the formation of secretion to be poured into the gland ducts; in the thyroid and suprarenal bodies we find cells forming special materials which are passed into blood or lymph. The hepatic cells do both, and it should be borne in mind that possibly all gland-cells do. In fact it has already been pointed out that the pancreas has still another function than the formation of pancreatic juice. As regards the liver-cells, we naturally ask whether the two processes, bile-making and glycogen-making, are distinct and independent activities, or whether bile and glycogen are simultaneous products of a single metabolic activity, as soap and glycerine are of the chemical process of soap-making: but to this question it is not possible yet to give a satisfactory answer.

The Source and Destination of Liver Glycogen. All foods are not equally efficacious in keeping up the stock of glycogen in the liver; fats by themselves are useless; proteids by themselves give a little; by far the most is formed on a diet rich in starch and sugar ; so it would seem that glycogen is mainly formed from carbohydrate materials absorbed from the alimentary canal and carried to the hepatic cells by the portal vein. The chief of these materials is probably glucose, since, although saliva and the amylolytic ferment of the pancreas convert starch into maltose $(C_{12}H_{22}O_{11} + H_2O)$, of the cane-sugar group, the intestinal secretion rapidly converts this into grape-sugar or glucose. This is taken up by the liver-cells, modified by them and stored as glycogen; and by their further activity from time to time reconverted into glucose and passed into the blood according to the needs of the Body in general. The cells then do distinctly chemical work on the carbohydrate material: possibly, indeed even probably, they build that supplied into their own living substance and then by partial breaking down of this, deposit some of it for a time as glycogen: and by further living activity turn this into glucose and send it on to the blood, when the

sugar in that liquid falls below a certain percentage. That the chief part of the glycogen found in the normal liver has its ultimate source in carbohydrate foods is shown by several facts. (1) Sugar if it exist in the blood in above a certain small percentage, passes out by the kidneys and appears in the urine, constituting the characteristic symptom of the disease called *diabetes*. In health, however, even after a meal very rich in carbohydrates, sugar rarely appears in the urine, and then but temporarily; so that the large quantity of it absorbed from the alimentary canal within a brief time under such circumstances, must be stopped somewhere before it reaches the general blood-current. (2) Glucose injected into one of the general veins of an animal, if in any quantity, soon appears in the urine; but the same amount injected into the portal vein, or one of its radicles, causes no diabetes, but an accumulation of glycogen in the liver. We may therefore conclude that the sugar absorbed from the alimentary canal is taken by the portal vein to the liver, and there converted into glycogen and stayed for a time; and later slowly passed on into the hepatic veins during the intervals between meals. Thus in spite of the intervals which elapse between meals the carbohydrate content of the blood is kept pretty constant: during digestion it is not suffered to rise very high, nor during ordinary periods of fasting to fall very much below the average.

In what form glycogen leaves the liver is not certain ; it might be dissolved out and carried off as such, or previously turned again into glucose and sent on in that form ; since the fresh liver-cells are capable of changing glycogen into glucose the latter view is the more probable. Analyses of portal and hepatic bloods, made with the view of determining whether more sugar was carried out of the liver during fasting than into it, are conflicting; and considering the great amount of blood which flows through the liver in twenty-four hours, a very slight increase of sugar (falling within the limits of error of the difficult quantitative determination of that substance in the blood) in the hepatic vein would represent a large total amount during the whole day. The main fact, however, remains that somehow this carbohydrate reserve in the liver is steadily carried off to be used elsewhere: and animal glycogen thus answers pretty much to vegetable starch, which, made in the green leaves, is dissolved and carried away

by the sap currents to distant and not green parts (as the grains of corn or tubers of a potato, which cannot make starch for themselves) and in them is again laid down in the form of solid starch grains, which are subsequently dissolved and used for the growth of the germinating seed or potato. Reasons have been given in an early part of this chapter for believing that the carbohydrate leaving the liver is not oxidized in the blood, but only after it has passed out of that into the organized tissue. Among these the muscles at least seem to get some, since a fresh muscle always contains glycogen, and even to retain it in normal amount after an animal has been starved for some time; the muscle-fibres then, so to speak, drawing on the balance with their banker (the liver) so long as there is any. When a muscle contracts, this glycogen disappears and some glucose appears, but not an amount equivalent to the glycogen used up; so that the working muscle, it is probable, uses this substance, among others, for its repair after each contraction.

How it is that the glycogen, which is so rapidly converted into grape-sugar by the dying liver, escapes such rapid conversion during life has not been satisfactorily answered. It may be that the metabolisms of the dying hepatic cell include processes which are an exaggeration of those occurring during normal life; in some such way as the production of myosin in dying muscle is apparently an exaggeration of chemical changes occurring in normal contracting muscle: or the glycogen in the living cell may not exist free, but combined with other portions of the cell substance so as to be protected; while, after death, *post-mortem* changes may rapidly liberate it in a condition to be acted upon.

Diabetes. The study of this disease throws some light upon the history of glycogen. Two distinct varieties of it are known; one in which sugar appears in the urine only when the patient takes carbohydrate foods; the other in which it is still excreted when he takes no such foods, and must therefore form sugar in his Body from substances not at all chemically allied to it. The more probable source of the sugar in the latter case is proteids; since some glycogen is found in the livers of animals fed on proteids only, while fats by themselves give none of it. It seems that the proteid molecule, in some complex way, is split up in the liver into a highly nitrogenized part (urea or an antecedent of urea) and

a nonazotized part, glycogen. On this view the more severe form of diabetes would be due to an increased activity of a normal proteid-decomposing function of the hepatic cells; and sometimes the urea and sugar in the urine of diabetics rise and fall together, thus seeming to indicate a community of origin. Diabetes dependent on carbohydrate food might be produced in several ways. The liver-cells might cease to stop the sugar and, letting it all pass on into the general circulation, suffer it to rise to such a percentage in the blood after a meal, that it attained the proportion in which the kidneys pass it out; or the tissues might cease to use their natural amount of sugar, and this, sent on steadily out of the liver, at last rise in the blood to the point of excretion. Or the liver might transform (into glucose) and pass on its glycogen faster than the other tissues used it, and so diabetes might arise; but this would only be temporary, lasting until the liver stock was used up by the rapid conversion. Artificially we can, in fact, produce diabetes in several of these ways; curari poisoning, for example, paralyzing the motor nerves, makes the skeletal muscles lie completely at rest, and so diminishes the glycogen consumption of the Body and produces diabetes. Carbon-monoxide poisoning produces diabetes also, presumably by checking bodily oxidation. Finally, pricking a certain spot in the *medulla oblongata* causes a temporary diabetes. This might conceivably be due to the fact that the operation injures that part of the vaso-motor centre which controls the muscular coat of the hepatic artery, and this artery, then dilating, carries so much blood through the liver that an excess of glycogen is carried off by the hepatic veins; and in favor of this opinion is the fact that if the splanchnic nerves be cut the whole arteries of the abdominal viscera dilate no diabetes follows. This has been explained as due to the fact that so many vessels are dilated that a great part of the blood of the Body accumulates in them, and there is in consequence no noticeably increased flow through the liver. Others, however, maintain that the *"piqûre"* diabetes (as that due to pricking the medulla is called) is due to irritation of trophic nerve-fibres originating there, and governing the rate at which the liver-cells produce glycogen or convert it into glucose. This latter view, though perhaps the less commonly accepted, is probably the more correct. The hepatic cells do not merely hold back

glucose carried through the liver so that it is there to be washed out by a greater blood-flow, but they feed on sugar and proteids and make glycogen; and this is later converted into glucose and carried off. Glycogen, except for its discharge into the blood instead of a gland duct, would then be comparable to the materials stored in the cells of the salivary and some other glands (Chap. XIX); and the transformation of such bodies into the specific element of a secretion we have already seen to be directly under the control of the nervous system, and almost entirely or quite independent of the simultaneous blood-flow.

The History of Fats. While glycogen forms a reserve store of material which is subject to rapid alterations, determined by meal-times, the fats are much more stable; their periods of fluctuation are regulated by days, weeks, or months of good or bad nutrition, and during starvation they are not so readily, or at least so rapidly, called upon as the hepatic glycogen. If we carry on the simile by which we compared the reserve in each cell to pocket-money, the glycogen would answer somewhat to a balance on the right side with a man's banker; while the fat would represent assets or securities not so rapidly realizable; as capital in business, or the cargoes afloat in the argosies of Antonio, the "Merchant of Venice." Fat, in fact, is slowly laid down in fat-cells and surrounded in these by a cell-wall, and, being itself insoluble in blood plasma or lymph, it must undergo chemical changes, which no doubt require some time, before it can be taken into the blood and carried off to other parts.

When adipose tissue is developing it is seen that undifferentiated cells in the connective tissues (especially areolar) show minute oil-drops in their protoplasm; these increase in size and ultimately fuse together and form one larger oil-droplet, while most of the original protoplasm disappears.

The oily matter would thus seem due to a chemical metamorphosis of the cell protoplasm, during which it gives rise to a non-azotized fatty residue which remains behind, and a highly nitrogenous part which is carried off. In many parts of the Body protoplasmic masses are subject to a similar but less complete metamorphosis; fatty degeneration of the heart, for example, is a more or less extensive replacement of the proper substance of its muscular fibres by fat-droplets; and the cream of milk and the oily matter of the sebaceous secre-

tion are due to a similar fatty degeneration in gland-cells. Moreover, careful feeding experiments undoubtedly show that fat can come from proteids; when an animal is very richly supplied with these all the nitrogen taken in them reappears in its excretions, but all the carbon does not; it is in part stored in the Body: and, since such feeding produces but little glycogen, this carbon can only be stored as fat.

While there is, then, no doubt that some fat may have a proteid origin, it is not certain that all has such. During digestion a great deal of fat is ordinarily absorbed, in a chemically unchanged state, from the alimentary canal; it is merely emulsified and carried off in minute drops by the chyle to be poured into the blood; and this fat might conceiveably be directly deposited, as such, in adipose tissue. There are, however, good reasons for supposing that all the fat in the Body is manufactured. The fat of a man, of a dog, and of a cat varies in the proportions of palmatin, stearin, margarin, and olein in it; and varies in just the same way if all be fed on the same kind of food, which could not be the case if the fat eaten were simply deposited unchanged. Moreover, if an animal be fed on a diet containing one kind of fat only, say olein, but a very slightly increased percentage of that particular fatty substance is found in its adipose tissue, which goes to show that if fats come from fats eaten, these latter are first pulled to bits by the living cells and built up again into the forms normal to the animal; so that, even with fatty food, the fats stored up seem to be in most part manufactured in the Body.

In still another way it is proved that fats can be constructed in the Body. In animals fed for slaughter, the total fat stored up in them during the process is greatly in excess of that taken with their food during the same time. For example, a fattening pig may store up nearly five hundred parts of fat for every hundred in its food, and this fat must be made from proteids or carbohydrates. Whether it can come from the latter is still perhaps an open question; for, while all fattening foods are rich in starch or similar bodies, there are considerable chemical difficulties in supposing an origin of fats from such; and it is on the whole more probable that they simply act by sparing from use fats simultaneously formed or stored in the body, and which would have otherwise been called upon. They make glycogen, and this

shelters the fats. Liebig, indeed, in a very celebrated dis-cussion, maintained that fats were formed from carbohydrates. He showed that a cow gave out more butter in its milk than it received fats in its food; and Huber, the blind naturalist, showed that bees still made wax (a fatty body) for a time when fed on pure sugar; and indefinitely when fed on honey. Consequently, for a long time, an origin of fats from carbo-hydrates was supposed to be proved; but their possible origin from proteids (a possibility now shown to be a certainty) was neglected, and the validity of the above proofs of their carbo-hydrate origin is thus upset. The cow may have made its butter from proteids; the bees, fed on sugar, their wax for a time from proteids already in their bodies; and, indefinitely, when fed on honey, from the proteids in that substance. Moreover, animals (ducks) fed on abundant rice, which con-tains much carbohydrate but very little proteid or fat, remain lean; while if some fat be added they lay up fat.

Persons who fatten cattle for the butcher find that the foods useful for the purpose all contain proteids, carbohy-drates, and fats, and that rapid fattening is only obtained with foods containing a good deal of fat; as oilcake, milk, or Indian corn. Taking all the facts into account we shall probably not be wrong in concluding that nearly all the bodily fat is manufactured either from fats or proteids; from fats easier than from anything else, but when much proteid is eaten some is made from it also. Carbohydrates alone do not fatten; the animal body cannot make its pal-matin, etc., out of them. Nevertheless they are, indirectly, important fattening foods when given with others, since, being oxidized instead of it, they protect the fat formed.

Dietetics. That "one man's meat may be another man's poison" is a familiar saying, and one that, no doubt, ex-presses a certain amount of truth; but the difference probably depends on the varying digestive powers of individuals rather than on peculiarities in their laws of cell nutrition: we all need about the same amount of proteids, fats, and carbohydrates for each kilogram of body weight; but all of us cannot digest the same varieties of them equally well: it is also a matter of common experience that some foods have peculiar, almost poisonous, effects on certain persons. Some people are made ill by mutton, which the majority digest better than beef.

The proper diet must necessarily vary, at least as to amount, with the work done; whether it should vary in kind with the nature of the work is not so certain. Provided a man gets enough proteids to balance those lost in the wear and tear of his tissues, it probably matters little whether he gets for oxidation and the liberation of energy either fats or carbohydrates, or even excess of proteids themselves; any one of the three will allow him to work either his brain or his muscles, and to maintain his temperature. Proteids, however, are wasteful foods for mere energy-yielding purposes: in the first place, they are more costly than the others; secondly, they are incompletely oxidized in the Body; and, thirdly, it is probably more laborious to the system to get rid of urea than of the carbon dioxide and water, which alone are yielded by the oxidation of fats and carbohydrates. Between fats and carbohydrates similar considerations lead to a use of the latter when practicable: starch is more easily utilized in the Body than fats, as shown by the manner in which it protects the latter from oxidation; and a given weight of starch fully oxidized in the Body will liberate about one half as much energy as the same amount of butter, while it costs considerably less than half the money. Also, starch is more easily digested than fats by most persons: children especially are apt to be fond of starchy or saccharine foods and to loathe fats; and the appetite in such cases is a good guide. As a rule the people of the United States differ very markedly from the English in their love of sweet foods of all kinds; whether this is correlated with their characteristic activity, calling for some food that can be rapidly used, is an interesting question.

It is certain that no general rules for the best dietary for all persons can be formulated, but on broad principles the best diet is that which contains just the amount of proteid necessary for tissue repair, and so much carbohydrates as can be well digested; the balance needed, if any, being made up by fats and gelatinoids. Such a food would be the cheapest; that is, the supplying of it would call for less of the time and energy of the nation using it, and leave more work to spare for other pursuits than food production—for all the arts which make life agreeable and worth living, and which elevate civilized man above the merely material life of the savage whose time is devoted to catching and eating.

We have high authority for saying that man does not live by bread alone; in other words, his highest development is impossible when he is totally absorbed in "keeping body and soul together," and the more labor that can be spared from getting enough food the better chance has he, if he use his leisure rightly, of becoming a more worthy man. While there is, thus, a theoretically best diet, it is nevertheless impossible to say what that is for each individual; but what the general experience is may be approximately gathered by taking an average of the dietaries of a number of public institutions in which the health of many people is maintained as economically as possible. Such an examination made by Moleschott gives us as its result a diet containing daily—

Proteids	80 grams	or	465	grains
Fats	84 "	or	1,300	"
Carbohydrates	404 "	or	6,262	"
Salts	30 "	or	465	"
Water	2800 "	or	43,400	"

People in easy circumstances take as a rule more proteids and fats and less amyloids; and this selection, when a choice is possible, probably indicates that such a diet is the better one: the proteids in the above table seem especially deficient. Experimenting on himself the physiologist Ranke found that when he was in good health, neither gaining nor losing weight, and excreting daily as much nitrogen as he took in food, he maintained this condition of equilibrium on a diet containing

Proteids	100 grams	(	1550	grains)
Fats	100 "	(	1550	")
Carbohydrates	240 "	(	3720	")
Salts	25 "	(	437	")
Water	2600 "	(	40,400	")

Other experimenters have since arrived at very similar results; and such a diet is probably about the normal for persons of our race living in a temperate climate.

CHAPTER XXX.

THE PRODUCTION AND REGULATION OF THE HEAT OF THE BODY.

Cold- and Warm-blooded Animals. All animals, so long as they are alive, are the seat of chemical changes by which heat is liberated; hence all tend to be somewhat warmer than their ordinary surroundings, though the difference may not be noticeable unless the heat production is considerable. A frog or a fish is a little hotter than the air or water in which it lives, but not much; the little heat that it produces is lost, by radiation or conduction, almost at once. Hence such animals have no proper temperature of their own; on a warm day they are warm, on a cold day cold, and are accordingly known as *changeable-temperatured (poikilo-thermous)* or, in ordinary language, "cold-blooded" animals. Man and other mammals, as well as birds, on the contrary, are the seat of very active chemical changes by which much heat is produced, and so maintain a tolerably uniform temperature of their own, much as a fire does whether it be burning in a warm or a cold room; the heat production during any given time balancing the loss, a normal body temperature is maintained, and usually one considerably higher than that of the medium in which they live; such animals are commonly named "warm-blooded." This name, however, does not properly express the facts; a lizard basking in the sun on a warm summer's day may be quite as hot as a man usually is; but on the cold day the lizard becomes cold, while the average temperature of the healthy Human Body is, within a degree, the same in winter or summer; within the arctic circle or on the equator. Hence it is better to call such animals "*homothermous*" or of uniform temperature.

Moderate warmth accelerates protoplasmic activity; compare a frog dormant in the winter with the same animal active in the warm months: what is true of the whole frog is true of each of its living cells. Its muscles contract more

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rapidly when warmed, and the white corpuscles of its blood when heated up to the temperature of the Human Body are seen (with the microscope) to exhibit much more active amœboid movements than they do at the temperature of frog's blood. In summer a frog or other cold-blooded animal uses much more oxygen and evolves much more carbon dioxide than in winter, as shown not only by direct measurements of its gaseous exchanges, but by the fact that in winter a frog can live a long time after its lungs have been removed (being able to breathe sufficiently through its moist skin), while in warm weather it dies of asphyxia very soon after the same loss. The warmer weather puts its tissues in a more active state; and so the amount of work the animal does, and therefore the amount of oxygen it needs, depend to a great extent upon the temperature of the medium in which it is living. With the warm-blooded animal the reverse is the case. Within very wide limits of exposure to heat or cold it maintains its temperature at that at which its tissues live best; accordingly in cold weather it uses more oxygen and sets free more carbon dioxide because it needs a more active internal combustion to compensate for its greater loss of heat to the exterior. And it does not become warmer in warm weather, partly because its oxidations are less than in cold (other things being equal), and partly because of physiological arrangements by which it loses heat faster from its body. In fact the living tissues of a man may be compared to hothouse plants, living in an artificially maintained temperature; but they differ from the plants in the fact that they themselves are the seats of the combustions by which the temperature is kept up. Since, within wide limits, the Human Body retains the same temperature no matter whether it be in cold or warm surroundings, it is clear that it must possess an accurate arrangement for heat regulation; either by controlling the production of heat in it, or the loss of heat from it, or both.

The Temperature of the Body. The parts of the Body are all either in contact with one another directly or, if not, at least indirectly through the blood, which, flowing from part to part, carries heat from warmer to colder regions. Thus, although at one time one group of muscles may especially work, liberating heat, and at other times another, or the muscles may be at rest and the glands the seat of active oxidation, the temperature of the whole Body is kept pretty much the same. The skin, however, which is in direct con-

tact with external bodies, usually colder than itself, is cooler than the internal organs; its temperature in health is from 36° to 37° C. (96.8–98.5° F.), being warmer in more protected parts, as the hollow of the armpit. In internal organs, as the liver and brain, the temperature is higher; about 43° C. (107° F.) in health. In the lungs there is a certain quantity of heat liberated when oxygen combines with hæmoglobin, but this is more than counterbalanced by loss of the heat carried out by the expired air and that used up in evaporating the water carried out in the breath, so the blood returned to the heart by the pulmonary veins is slightly colder than that carried from the right side of the heart to the lungs.

The Sources of Animal Heat. Apart from heat received from its surroundings in hot food and drink the sources of heat in the Body are twofold—direct and indirect. Heat is directly produced wherever oxidation is taking place; and, since almost invariably the chemically degrading or katabolic processes going on in a living organ exceed the anabolic, the living tissues at rest produce heat as one result of the chemical changes supplying them with energy for the maintenance of their vitality: and whenever an organ is active and its chemical metamorphoses are increased it becomes hotter: a secreting gland or a contracting muscle is warmer than a resting one, and the venous blood leaving noticeably warmer than the arterial supplied to it. Indirectly, heat is developed within the Body by the transformation of other forms of energy: mainly mechanical work, but also of electricity. All movements of parts of the Body which do not move it in space or move external objects, are transformed into heat within it; and the energy they represent is lost in that form. Every cardiac contraction sets the blood in movement, and this motion is for the most part turned into heat within the Body by friction within the blood-vessels. The same transformation of energy occurs with respect to the movements of the alimentary canal, except in so far as they expel matters from the Body; and every muscle in contracting has part of the mechanical energy expended by it turned into heat by friction against neighboring parts. Similarly the movements of cilia and of amœboid cells are for the most part converted in the Body into heat. The muscles and nerves are also the seats of manifestations of electricity, which, though small in amount, for the most part do not leave the Body in that form but are first converted into heat.

The Energy Lost by the Body in Twenty-four Hours
Practically speaking, the Body only loses energy in two
forms; as heat and mechanical work: by applying conduct-
ors to different parts of its surface small amounts of elec-
tricity can be carried off, but the amount is quite trivial in
comparison with the total daily energy expenditure. During
complete rest, that is, when no more work is done than that
necessary for the maintenance of life, nearly all the loss takes
the form of heat. The absolute amount of this will vary
with the surrounding temperature and other conditions, but
on an average a man loses, during a day of rest, 2700 calories;
that is enough to raise 2700 kilograms (5940 lbs.) of water
from 0° to 1° C. (from 32° to 33 8° F.); otherwise expressed,
this amount of heat would boil 27 kilos (59.4 lbs.) of ice-cold
water. This does not quite represent all the energy lost by
the Body in that time: since a small proportion is lost as
mechanical work in moving the clothes and air by the respir-
atory movements, and even by the beat of the heart, which at
each systole pushes out the chest-wall a little and moves the
things in contact with it. The working Body liberates and
loses much more energy; part as mechanical work done on
external objects, part as increased heat radiated or conducted
from the surface, or carried off by the expired air in the
quickened respirations. Every one knows that he feels
warmer when he takes exercise, and this is due to the greater
amount of blood then carried to the skin and raising for the
time its temperature. The general temperature of the Body
as measured in the mouth is not at all or only very slightly
raised, however, as the greater loss of heat from the skin keeps
the average temperature of the blood at its normal level. This
greater loss corresponding to the greater production has been
measured on persons enclosed in specially constructed calori-
meters; and though there are considerable difficulties in the
way of getting quite accurate results, the measurements show
that the heat produced and lost in a day of moderate work is
about one third greater than that in a day of rest. The fol-
lowing table gives more definite numbers:

	Day of Rest.		Day of Work.		
	Rest 16 hrs.	Sleep 8 hrs.	Rest 8 hrs.	Work 8 hrs.	Sleep 8 hrs.
Heat-units (calo- ries) produced.	2470 4	320	1235.2	2169.6	320.
	2790.4 (10,885 Fah.-lb. heat-units.)		3724.8 (14,598 Fah. lb. heat-units.)		

The mechanical work done on the working day represented in addition an expenditure of energy of 213,344 kilogrammeters, which is equal to 502 calories. Of the excess heat in the working day, part is directly produced by the increased chemical changes in the quicker working heart and respiratory muscles, and the other muscles set at work; while part is indirectly due to heat arising from increased friction in the blood-vessels as the blood is driven faster around them, and to friction of the various muscles used. The average cardiac work in twenty-four hours is about 60,000 kilogrammeters; that of the respiratory muscles about 14,000; and since nearly all of both is turned finally into heat within the Body, we have 74,000 kilogrammeters of energy answering to about 174 calories (6786 Fah.-lb. units) indirectly produced in the resting Body daily from these sources.

Of 100 parts of heat lost from the resting Body, about 74.7 are carried off in radiation or conduction from the skin. 14.5 are carried off in evaporation from the skin.

5.4 "   "   "   "   "   " lungs.

3.6 "   "   " expired air.

1.8 "   "   " the excretions.

In a day of average work, of every 100 parts of energy lost in any form from the Body—

1–2 go as heat in the excreta.

3–4 in heating the expired air.

20–30 in evaporating water from the lungs and skin.

60–75 in heat radiated or conducted from the surfaces and in external mechanical work.

It is obvious, however, that such numbers are only rough approximations and must vary greatly with the temperature and moisture of the surrounding air, the rate of respiration, and other circumstances.

The Superiority of the Body as a Working Machine. During eight hours of work we find (see table) the Body loses 2169.6 calories of energy as heat, and can do simultaneously work equivalent to 502 calories. So of all the energy lost from it in that time about ¼ may take the form of mechanical work; this is a very large proportion of the total energy expended, being a much higher percentage than that given by ordinary machines. The best steam-engines can utilize as mechanical work only about ⅛ of the total energy liberated in them and lost from them in a given time, the

remainder is transmitted directly as heat to the exterior, and is lost to the engine for all useful purposes.

The Maintenance of an Average Temperature. This is necessary for the continuance of the life of a warm-blooded animal; should the temperature rise above certain limits chemical changes, incompatible with life, occur in the tissues; for example at about 49° C. (120° F.) the muscles begin to become rigid. On the other hand, death ensues if the Body be cooled down to about 19° C. (66° F.). Hence the need of means for getting rid of excess heat, and of protection from excessive cooling. Either end may be gained in two ways: by altering the rate at which heat is lost or that at which it is produced. As regards heat-loss, by far the most important regulating organ is the skin: under ordinary circumstances nearly 90 per cent of the total heat given off from the Body in 24 hours goes by the skin (73 by radiation and conduction, 14.5 by evaporation). This loss may be controlled—

1. By *clothing ;* we naturally wear more in cold and less in warm weather; the effect of clothes being, of course, not to warm the Body but to diminish the rate at which the heat produced in it is lost.

2. Increased temperature of the surrounding medium increases the activity of the heart and lungs. A hastened circulation by itself does not, as already pointed out (Chap. XXVI), increase the general tissue activity of the Body, or the oxidations occurring in it, and so, apart from the harder-working heart itself, does not influence the amount of heat liberated in the Body during a given time: but the more rapid blood-flow through the skin carries more of that fluid through this cool surface in each minute and in that way increases the loss of heat. The quickened respirations, too, increase the evaporation of water from the lungs and, thus, the loss of heat.

3. Warmth, mainly through reflex vaso-moter actions leads to dilatation of the skin-vessels and cold to contraction. In a warm room the vessels on the surface dilate as shown by its redness, while in a cold atmosphere they contract and the skin becomes pale. But the more blood that flows through the skin the greater will be the heat lost from the surface—and *vice versa.*

4. Heat induces sweating and cold checks it; the heat appears to act, partly, reflexly through afferent cutaneous

nerve fibres exciting the sweat-centres from which the secretory nerves for the sudoriparous glands arise and, partly, directly on those centres, as they are thrown into activity, at least in health, as soon as the temperature of the blood flowing through the spinal cord is raised. In fever of course we may have a high temperature with a dry non-sweating skin. The more there is sweat poured out, the more heat is used up in evaporating it and the more the Body is cooled.

5. Our sensations induce us to add to or diminish the heat in the Body according to circumstances; as by cold or warm baths, and iced or hot drinks.

As regards temperature-regulation by modifying the rate of heart production in the Body, the following points may be noted; on the whole, such regulation is far less important than that brought about by changes in the rate of loss, since the necessary vital work of the Body always necessitates the continuance of oxidative processes which liberate a tolerably large quantity of heat. The Body cannot therefore be cooled by diminishing such oxidations; nor, on the other hand, can it be safely warmed by largely increasing them. Still, within certain limits, the heat production may be controlled in several ways :

1. Cold increases hunger; and increased ingestion of food increases bodily oxidation, as shown by the greater amount of carbon dioxide excreted in the hours succeeding a meal. This increase is probably due to the activity into which the digestive organs and such metabolic organs as the liver are thrown; hepatic-vein blood is about one degree centigrade (nearly two degrees Fahrenheit) warmer than portal-vein blood, and during digestion much more blood flows through the liver.

2. Cold inclines us to voluntary exercise; warmth to muscular idleness; and the more the muscles are worked the more heat is produced in the Body.

3. Cold tends to produce involuntary muscular movements, and so increased heat production; as chattering of the teeth and shivering.

4. Cold applied to the skin increases the bodily chemical metamorphoses and heat production. At least the temperature in the armpit rises at first on entering a cold bath, though the heat carried off from the surface soon overbalances its increased production. The phenomenon may,

however, be explained in another way, the rise being attributed to a sudden diminution of loss from more exposed parts of the skin, dependent on contraction of the cutaneous arteries. In some cases, however, the temporary rise is accompanied by an increased excretion of carbon dioxide, which would indicate that the surface cooling does really increase the oxidations of the Body.

5. Certain drugs, as salicylic acid, and perhaps quinine, diminish the heat production of the Body. Their mode of action is still obscure.

On the whole, however, the direct heat-regulating mech anisms of the Human Body itself are not very efficient, especially as protections against excessive cooling. Man needs to supplement them by the use of clothing, fuel, and exercise.

Local Temperatures. Although, by the means above described, a wonderfully uniform bodily temperature is maintained, and by the circulating blood all parts are kept at nearly the same warmth, variations in both respects do occur. The arrangements for equalization are not by any means fully efficient. External parts, as the skin, the lungs (which are really external in the sense of being in contact with the air), the mouth, and the nose chambers, are always cooler than internal; and even all parts of the skin have not the same temperature, such hollows as the armpit being warmer than more exposed regions. On the other hand, a secreting gland or a working muscle becomes warmer, for the time, than the rest of the Body, because more heat is liberated in it than is carried off by the blood flowing through. In such organs the venous blood leaving is warmer than the arterial coming to them; while the reverse is the case with parts, like the skin, in which the blood is cooled. An organ colder than the blood is of course warmed by an increase in its circulation, as seen in the local rise of temperature in the skin of the face in blushing.

Thermogenic Nerves. All nerves, such as motor or secretory, which can throw working tissues into activity are in a certain sense thermogenic nerves, since they excite increased oxidation and heat production in the parts under their control. A true, purely thermogenic nerve would be one which increased the heat production in a tissue without otherwise throwing it into activity; and whether such exist

is still undecided. Certain phenomena of disease, however, seem to render their existence probable. If we return for a moment to our former comparison of the working Body to a steam-engine, such nerves might be regarded as agencies increasing its rate of rusting without setting it at work. The oxidation of the iron would develop some heat, but by processes useless to the steam-engine, although such are, in moderation, essential to living cells; the vitality of these, even when they rest, seems to necessitate a constant, if small, breaking down of their substance. In an amœboid cell no doubt such processes occur quite independently of the nervous system; but in more differentiated tissues they may be controlled by it. Just as a muscle does not normally contract unless excited through its nerve, although a white blood-corpuscle does, so may the natural nutritive processes of the muscle-fibre in its resting condition be dependent on the nerves going to it. If these be abnormally excited the muscle will break down its protoplasm faster than it constructs it, and consequently waste; at the same time the increased chemical degradation of its substance will elevate its temperature. Febrile conditions, in which many tissues waste, without any unusual manifestation of their normal physiological activity, would thus be readily accounted for as due to superexcitation of the thermogenic nerves and nerve-centre.

The condition of *fever* or *pyrexia,* as an abnormally high temperature is named, could conceivably be brought about by increased heat production, decreased heat loss, or both; or by a greater increase of production than of loss. Direct experiments on animals prove that there is always increased production of heat, in febrile diseases. This is shown by the fact that the animal uses more oxygen and gives off more carbon dioxide in a given time than when in health. It also usually gives off more heat, but not enough to compensate for the increase of oxidative processes going on in its body, and so its temperature rises. The regulating mechanism which in health keeps heat production and heat dissipation proportionate is out of gear. As regards the increased heat formation in pyrexial conditions, there is some reason to believe that it is usually due to excitation by morbid products of thermogenic centres lying in the corpora striata or optic thalami. Pricking those regions of the brain of an animal causes greatly in-

creased heat formation in its body. This has been interpreted either as due to the excitation of thermogenic nerve-centres which then stir up increased katabolisms in the tissues or to injury and paralysis of inhibitory centres which normally hold tissue metabolisms in check. The fact that a similar result may be obtained by electrical stimulation of this region of the brain is in favor of the excitation theory, but the possibility of the existence also of febrile paralysis of nerve-cells which normally inhibit a heat-production centre should be borne in mind.

Clothing. While the majority of other warm-blooded animals have coats of their own, formed of hairs or feathers, over most of man's Body his capillary coating is merely rudimentary and has lost nearly all physiological importance as a protection from cold; except in tropical regions he has to protect himself by artificial garments, which his æsthetic sense has led him to utilize also for purposes of adornment. Here, however, we must confine ourselves to clothes from a physiological point of view. In civilized societies every one is required to cover most of his Body with something, and the question is what is the best covering; the answer will vary, of course, with the climatic conditions of the country dwelt in. In warm countries, clothing, in general terms, should allow free radiation or conduction of heat from the surface; in cold it should do the reverse; and in temperate climates, with varying temperatures, it should vary with the season. If the surface of the Body be exposed so that currents of air can freely traverse it much more heat will be carried off (under those usual conditions in which the air is cooler than the skin) than if a stationary layer of air be maintained in contact with the surface. As every one knows, a "draught" cools much faster than air of the same temperature not in motion. All clothing, therefore, tends to keep up the temperature of the Body by checking the renewal of the layer of air in contact with it. Apart from this, however, clothes fall into two great groups: those which are good, and those which are bad, conductors of heat. The former allow changes in the external temperature to cool or heat rapidly the air stratum in actual contact with the Body, while the latter only permit these changes to act more slowly. Of the materials used for clothes, linen is a good conductor;

calico not quite so good; and silk, wool, and fur are bad conductors.

Whenever the surface of the Body is suddenly chilled the skin-vessels are contracted and those of internal parts reflexly dilated; hence internal organs tend to become *congested;* this within limits is a protective physiological process, but if excessive it readily passes into the diseased state known as *inflammation.* When hot, therefore, the most unadvisable thing to do is to sit in a draught, throw off the clothing, or in other ways to strive to get suddenly cooled. Moreover, while in the American summer it is tolerably safe to wear good-conducting garments, and few people take cold then, this is by no means safe in the spring or autumn, when the temperature of the air is apt to vary considerably within the course of a day. A person going out, clad only for a warm morning, may have to return in a very much colder evening; and if his clothes be not such as to prevent a sudden surface chill, will get off lightly if he only " take " one of the colds so prevalent at those seasons. In the great majority of cases, no doubt, he suffers nothing worse, but persons, especially of the female sex, often thus acquire far more serious diseases. When sudden changes of temperature are at all probable, even if the prevailing weather be warm, the trunk of the Body should be always protected by some tolerably close-fitting garment of non-conducting material. Those whose skins are irritated by anything but linen should wear immediately outside the under-garments a jacket of silken or woollen material. In mid-winter comparatively few people take cold, because all then wear thick and nonconducting clothing of some kind.

CHAPTER XXXI.

SENSATION AND SENSE-ORGANS.

The Subjective Functions of the Nervous System.
Changes in many parts of our Bodies are accompanied or
followed by those states of consciousness which we call *sen-
sations.* All such sensitive parts are in connection, direct
or indirect, with the brain, by certain afferent nerve-fibres
called *sensory.* Since all feeling is lost in any region of the
Body when this connecting path is severed, it is clear that
all sensations, whatever their primary exciting cause, are
finally dependent on conditions of the central nervous system.
Hitherto we have studied this as its activities are revealed
through movements which it excites or prevents; we have
seen it, directly or reflexly, cause muscles to contract, glands
to secrete, or the pulsations of the heart to cease; we have
viewed it *objectively,* as a motion-regulating apparatus. Now
we have to turn to another side and consider it (or parts of
it) as influencing the states of consciousness of its possessor:
this study of the *subjective* activities of the nervous system is
one of much greater difficulty.

It may be objected that considerations concerning states
of feeling have no proper place in a treatise on Anatomy
and Physiology; that, since we cannot form the beginning
of a conception how a certain state of the nervous system
causes the feeling redness, another the feeling blueness, and
a third the emotion anger, all examination of mental phe-
nomena should be excluded from the sciences dealing with
the structure and properties of living things. But, although
we cannot imagine how a nervous state (*neurosis*) gives rise
to a conscious state (*psychosis*), we do know this, that dis-
tinct phenomena of consciousness never come under our
observation apart from a nervous system, and so are pre-
sumably, in some way, endowments of it; we are, therefore,
justified in calling them properties of the nervous system;

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and their examination, especially with respect to what nerve-parts are concerned with different mental states, and what changes in the former are associated with given phenomena in the latter, forms properly a part of Physiology. Whether masses of protoplasm, before the differentiation of definite nerve-tissues, possess some ill-defined sort of consciousness, as they possess an indefinite contractility before they have been modified into muscular fibres, may for the present be left undecided: though those who accept the doctrine of evolution will be inclined to assent to the proposition.

While, however, the physiologist has a right to be heard on questions relating to our mental faculties, it is nevertheless true that many laws of thought have been established concerning which our present knowledge of the laws of the nervous system gives us no clue; the science of Psychology has thus a well-founded claim to an independent existence. But, in so far as its results are confined merely to the successions and connections of mental states, as established by observation, they are merely descriptions, and not explanations in a scientific sense: we know that so many mental phenomena have necessary material antecedents and concomitants in nervous changes, that we are justified in believing that all have such, and in continuing to seek for them. We do not know at all how an electric current sent round a bar of soft iron makes it magnetic; we only know that the one change is accompanied by the other; but we say we have explained the magnetism of a piece of iron if we have found an electric current circulating around it. Similarly, we do not know how a nervous change causes a mental state, but we have not explained the mental state until we nave found the nervous state associated with it and how that nervous state was produced.

As yet it is only with respect to some of the simplest states of consciousness that we know much of the necessary physiological antecedents, and among these our sensations are the best investigated. As regards such mental phenomena as the Association of Ideas and Memory, physiology can give us some light; but so far as others, such as the Will and the Emotions, are concerned, it has at present little to offer. The phenomena of Sensation, therefore, occupy at present a much larger portion of physiological works than all other mental facts put together.

Common Sensation and Organs of Special Sense. A sensory nerve is one which, when stimulated, arouses, or may arouse, a *sensation* in its possessor. The stimulant is in all cases some form of motion, molar (e.g., mechanical pressure) or molecular (as ethereal vibrations or chemical changes). Since all our nerves lie within our Bodies as circumscribed by the skin, and are excited within them, one might *a priori* be inclined to suppose that the cause of all sensations would appear to be within our Bodies themselves; that the thing *felt* would be a modified portion of the *feeler*. This is the case with regard to many sensations; a headache, toothache, or earache gives us no idea of any external object; it merely suggests to each of us a particular state of a sensitive portion of *myself*. As regards many sensations, however, this is not so; they suggest to us external causes, to properties of which, and not to states of our Bodies, we ascribe them; and so they lead us to the conception of an external universe. A knife laid on the skin produces changes in it which lead us to think not of a state of our skin, but of states of some object outside the skin; we believe we feel a cold heavy hard thing in contact with it. Nevertheless we have no sensory nerves going into the knife and informing us directly of its condition; what we really feel are the modifications of our Body produced by it, although we irresistibly think of them as properties of the knife—of some object that is no part of the Body, and not of them as states of the latter. Let now the knife cut through the skin; we feel no more *knife*, but experience *pain*, which we think of as a condition of ourselves. We do not say the knife is painful, but that our finger is, and yet we have, so far as sensation goes, as much reason to call the knife painful as cold. Applied one way it produced local changes arousing a sensation of cold, and in another local changes causing a sensation of pain. Nevertheless in the one case we speak of the cold as being in the knife, and in the other of the pain as being in the finger.

Sensitive parts, such as the surface of the skin, through which we get, or believe we get, information about outer things, are of far more intellectual value to us than sensitive parts, such as the subcutaneous tissue into which the knife may cut, which give us only sensations referred to conditions of our Bodies. The former are called *Sense-organs* proper,

or *Organs of Special Sense ;* the latter are *sensitive parts,* or *Organs of Common Sensation.*

The Peripheral Reference of our Sensations. The fact that we refer certain sensations to external causes is only one case of a more general law, in accordance with which we do not ascribe our sensations, as regards their locality, to the brain, where the neurosis is accompanied by the sensation, but to a peripheral part. With respect to the brain, other parts of the Body are external objects as much as the rest of the material universe, yet we locate the majority of our common sensations at the places where the sensory nerves concerned are irritated, and not in the brain. Even if a nerve-trunk be stimulated in the middle of its course, we refer the resulting sensation to its outer endings. A blow on the inside of the elbow-joint, injuring the ulnar nerve, produces not only a local pain, but a sense of tingling ascribed to the fingers to which the ends of the fibres go. Persons with amputated limbs have feelings in their fingers and toes long after they have been lost, if the nerve-trunks in the stump be irritated. To explain such facts we must trench on the ground of Psychology, and so they cannot be fully discussed here; but they are commonly ascribed to the results of experience. The events of life have taught us that in the great majority of instances the sensory impulses which excite a given tactile sensation, for example, have acted upon the tip of a finger. The sensation goes when the finger is removed, and returns when it is replaced; and the eye confirms the contact of the external object with the finger-tip when we get the tactile sensation in question. We thus come firmly to associate a particular region of the skin with a given sensation, and whenever afterwards the nerve-fibres coming from the finger are stimulated, no matter where in their course, we ascribe the origin of the sensation to some thing acting on the finger-tip.

The Differences between Sensations. In both groups of sensations, those derived through organs of special sense and those due to organs of common sensation, we distinguish kinds which are absolutely distinct for our consciousness, and not comparable mentally. We can never get confused between a sight, a sound, and a touch, nor between pain, hunger, and nausea; nor can we compare them with one another: each is *sui generis.* The fundamental difference

which thus separates one sensation from another is its *modality*. Sensations of the same modality may differ; but they shade imperceptibly into one another, and are comparable between themselves in two ways. First, as regards *quality*: while a high and a low pitched note are both auditory sensations, they are nevertheless different and yet intelligibly comparable; and so are blue, purple, and red objects. In the second place, sensations of the same modality are distinguishable and comparable as to amount or *intensity*: we readily recognize and compare a loud and a weak sound of the same pitch; a bright and feeble light of the same color; an acute and a slight pain of the same general character. Our sensations thus differ in the three aspects of *modality, quality within the same modality*, and *intensity*. Certain sensations also differ in what is known as the "*local signs*," a difference by which we tell a touch on one part of the skin from a similar touch on another; or an object exciting one part of the eye from an object like it, but in a different location in space and exciting another part of the visual surface.

As regards modality, we commonly distinguish five senses, those of sight, sound, touch, taste, and smell; to these, temperature must be added. The varieties of common sensation are also several; for example, pain, hunger, satiety, thirst, nausea, *malaise, bien être* ("feeling good"), fatigue. The *muscular sense* stands on the intermediate line between special and common sensations; we gather by it how much our various muscles are contracted: and so learn the position of various parts of the Body, on the one hand, and the resistance opposed to bodily movement by external objects, on the other. In fact, we cannot draw a sharp line between the special senses and common sensations: all the Body, we conclude from observations on the lower animals, is, at an early stage of its development, sensitive; very soon its cells separate themselves into an outer layer exposed to the action of external forces and an inner layer protected from them: and some of the former cells become especially *s[,]nsi/ive*. From them, as development proceeds, some are separated and buried beneath the surface to become the brain and spinal cord; of those which remain superficial, some are modified so that they (in the eye) become especially excited by ethereal vibrations; others (in the ear) become especially responsive to sound vibrations; others to slight chemical changes (in

mouth and nose), and others (in the skin) to variations in pressure or temperature.

All our sensations are thus modifications of one common primary sensibility, represented by that of the skin, or rather by the primitive representative of the skin in such an animal as the Hydra (see Zoology). The cutaneous sensations, being less differentiated, shade off more readily into the common sensibility of the other living tissues than do the activities of the highly differentiated cells in the eye and ear. We find, accordingly, that while a powerful pressure or a high temperature acting on the skin readily arouses a sensation of pain, that this is not the case with the more specialized visual and auditory organs. Their super-excitement may be disagreeable, but never passes into *pain*, in the ordinary sense of the word. Similarly the special skin sensations, touch and temperature, may sometimes be confounded, while a sound and a sight cannot be : the *modality* of the less modified skin-senses is less complete.

The study of comparative anatomy and development shows that the irritable parts of our sense-organs are but special differentiations of the primary external layer of cells which covered the Body when it was very young. Some of these cells become nerve end-organs in the eye, others end-organs in the ear, and so on; while others, less changed, remain in the skin as organs of touch and temperature; and so, from a general exterior surface responding equally readily to many external natural forces, we get a surface modified so that its various parts respond with different degrees of readiness to different external forces; and these modified parts constitute the essential portions of our organs of special sense. Every sense organ thus comes to have a special relationship to some one natural force or form of energy—is a specially irritable mechanism by which such a force is enabled to excite sensory nerves; and is, moreover, commonly supplemented by arrangements which, in the ordinary circumstances of life, prevent other forces from stimulating the nerves connected with it. Not all natural forces have sense-organs with reference to them developed in the Human Body; for example, we have no organ standing to electrical changes in the same relation that the eye does to light or the ear to sound.

The Essential Structure of a Sense-organ. In every sense-organ the fundamental part is one or more *end-organs*,

which are highly irritable tissues (p. 31), so constructed and so placed as to be normally acted on by some one of the modes of motion met with in the external world. A sensory apparatus requires in addition at least a brain-centre and a sensory nerve-fibre connecting this with the terminal apparatus; but one commonly finds accessory parts added. In the eye, e.g., we have arrangements for bringing to a focus the light rays which are to act on the end organs of the nerve-fibres; and in the ear are found similar subsidiary parts, to conduct sonorous vibrations to the end apparatus of the auditory nerve.

Seeing and hearing are the two most specialized senses; the stimuli usually arousing them are peculiar and quite distinct from the group of general nerve stimuli (Chap. XIII), while those most frequently, or naturally, acting upon our other sense-organs are not so peculiar; they are forces which act as general nerve stimuli when directly applied to nerve-fibres. The end-organs, however, as already pointed out, so increase the sensitiveness of the parts containing them that degrees of change in the exciting forces, which would be totally unable to directly stimulate the nerve-fibres, are appreciated. These terminal apparatuses are therefore as truly mechanisms enabling changes, which would not otherwise stimulate nerves, to excite them, as are the end-organs in the eye or ear.

The Cause of the Modality of our Sensations. Seeing that the external forces usually exciting our different sensations differ, and that the sensations do also, we might at first be inclined to believe that the latter difference depended on the former: that brightness differed from loudness because light was different from sound. In other words, we are apt to think that each sensation derives its specific character from some property of its external physical antecedent, and that our sensations answer in some way to, and represent more or less accurately, properties of the forms of energy arousing them. It is, however, quite easy to show that we have no sufficient logical warrant for such a belief. Light falling into the eye causes a sensation of luminosity, a feeling belonging to the visual group or modality; and, since usually nothing else excites such feelings and light entering the healthy eye always does, we come to believe that the physical agent light is something like our sensation of

luminosity. But, as we have already seen, no matter how we stimulate the optic nerve we still get visual sensations; close the eyes and press with a finger-nail on one eyelid; a sensation of touch is aroused where the finger meets the skin; but the pressure on the eyeball distorts it and stimulates the optic nerve-fibres in it also, and the result is a luminous patch seen in front of the eye in such a position as a bright body must occupy in space to radiate light to the stimulated part of the expansion of the optic nerve. Finding, then, the same kind of sensation, a visual one, produced by the totally different causes, pressure and light, we are led to doubt if the differences of modality in our sensations depend upon the differences of the natural forces arousing them; and this doubt is strengthened when we find still other forces giving rise to visual sensations. But then, since light and pressure, electricity and cutting, all cause visual sensations, we have no valid reason for supposing that light, more than either of the others, is really in any way like our sensation of light: or that sight-feeling differs from sound-feeling because objectively light differs from sound. The eye is an organ specially set apart to be excited by light, and accordingly so fixed as to have its nerve-fibres far more often excited by that form of force than by any other; but the fact that light sensations can be otherwise aroused shows plainly that their kind or character has nothing directly to do with any property of light. Just as by pinching or heating or galvanizing a motor nerve we can make the muscles attached to it contract, and the contraction has nothing in common with the excitant, so the visual sensation, as such, is independent of the stimulus arousing it and, of itself, tells us nothing concerning the kind of stimulus which has operated.

Differences in kind between external forces being thus eliminated as possible causes of the modalities of our sensations, we next naturally fall back upon differences in the sense-organs themselves. They do undoubtedly differ both in gross and microscopic structure, and the fact that pressure on the closed eye arouses a touch-feeling where the skin is compressed, and a sight-feeling where optic nerve-fibres are, might well be due to the fact that a peripheral touch-organ was different from a peripheral sight-organ, and the same force might therefore produce totally different effects on them and so cause different kinds of feelings. However,

here also closer examination shows that we must seek farther. Sensation is not produced in a sense-organ, but far away from it in the brain; the organ is merely an apparatus for generating nervous impulses. If the optic nerves be divided, no matter how perfect the eyeballs, no amount of light·will arouse visual sensations; if the spinal cord be cut in the middle of the back no pressure on the feet will cause a tactile or other feeling; though the skin, and its nerves and the lower half of the spinal cord be all intact. In all cases we find that if the nerve-paths between a sense-organ and the brain be severed no stimulation of the organ will call forth a sensation. The final production of this clearly depends, then, on something occurring in the brain, and so the kind of a sensation is presumably dependent upon brain events rather than on occurrences in sense-organs. Still it might be that something in the sense-organ caused one sensation to differ from another. Each organ might excite the brain in a different way and cause a different sensation, and so our sensations differ because our sense organs do. Such a view is, however, negatived by observations which show that perfectly characteristic sensations can be felt in the absence of the sense-organs through which they are normally excited. Persons whose eyeballs have been removed by the surgeon, or completely destroyed by disease, have frequently afterwards definite and unmistakable visual sensations, quite as characteristic as those which they had while still possessing the visual end organs. The tactile sensations felt in amputated limbs, already referred to, afford another example of the same fact. The persons still *feel* things touching their legs or lying between their long-lost toes; and the sensations are distinctly *tactile* and not in any way less different from visual or auditory sensations than are the touch-feelings following stimulation of those parts of the skin which are still possessed. It is, then, clear that the modality of our sensations is to be sought deeper than in properties of the end-organs of the nerves of each sense.

Properties of external forces and properties of peripheral nerve-organs being excluded as causes of differences in kind of sensation, we come next to the sensory nerve-fibres themselves. Is it because optic nerve-fibres are different from auditory nerve-fibres that luminous sensations are different from sonorous ? This question must be answered in

the negative, for we have already seen reason to believe that all nerve-fibres are alike in essential structure and that their properties are everywhere the same; that all they do is to transmit " nervous impulses " when excited, and that, no matter what the excitant, these impulses are molecular movements, always alike in kind, though they may differ in amount and in rate of succession. Since, then, all that the optic nerve does is to send nervous impulses to the brain, and all that the auditory and gustatory and tactile and olfactory nerve-fibres do is the same, and these impulses are all alike in kind, we cannot explain the difference in quality of visual and other sensations by any differences in property of the nerve-trunks concerned, any more than we could attempt to explain the facts that, in one case, an electric current sent through a thin platinum wire heats it, and, in another, sent through a solution of a salt decomposes it, by assuming that the different results depend on differences in the conducting copper wires, which may be absolutely alike in the two cases.

We are thus driven to conclude that our sensations primarily differ because different central nerve-organs in the brain are concerned in their production. That just as an efferent nerve-fibre will, when stimulated, cause a secretion if it go to a gland-cell, and a contraction if it go to a muscle-fibre, so an optic nerve-fibre, carrying impulses to one brain apparatus and exciting it, will cause a visual sensation, and a gustatory nerve-fibre, connected with another brain-centre, a taste sensation. In other words, our kinds of sensation depend fundamentally on the properties of our own cerebral nervous system. For each special sense we have a nervous apparatus with its peripheral terminal organs, its nerve-fibres, and its brain-centres; and the excitement of this apparatus, no matter in what way, causes a sensation of a given modality, determined by the properties of its central portion. Usually the apparatus is excited by one particular force acting first on its peripheral organs, but it may be aroused by stimulating its nerve-fibres directly or, as in certain diseased states (delirium), or under the action of certain drugs, by direct excitation of the centres. The sensations of dreams, frequently so vivid, and hallucinations, are also probably in many cases due to direct excitation of the central organs of sensory apparatuses, though no doubt also often due to peripheral stimulation. But no matter how or where the appa-

ratus is excited, provided a sensation is produced it is always of the modality of that sense apparatus.

While in the more specialized senses the modality of the sensation can be ascribed only to brain properties (so that we may be pretty sure that a man, the inner end of whose optic nerve was in physiological continuity with the outer end of his auditory, and the inner end of his auditory with the outer end of his optic, would hear a picture and see a symphony), yet, conceivably, differences in the rhythm or intensity of afferent nervous impulses might cause differences in modality in less differentiated senses. Until quite recently it has been considered possible that tactile and temperature sensations were but extremes of one general kind of feeling; that they were of the same " modality; " and comparable, for example, to the sensations of yellow and blue in the visual set of feelings. This view has now been definitely proved to be inadmissible (Chap. XXXV). The points of the skin which arouse in us the sensations of touch, heat, and cold are all distinct; each one when stimulated gives rise to only one kind of sensation, if any; and always the same kind. A heavy pressure, gradually increased, arouses sensations which pass imperceptibly from touch to pain, and this result may be due to the fact that regular and orderly afferent impulses, determined through tactile nerve-endings, excite the centre in one way; while irregular, disorderly, and violent impulses, originated when the pressure is great enough to directly excite nerve-trunks beneath the skin, may cause a different sensation; much as musical notes properly combined may cause pleasure, but all clashed together may cause suffering, although the same brain-centres are stimulated in the two cases. The pain from a heavy weight may, however, be due to the fact that it excites a different set of nerve-fibres than those connected with tactile feeling, and gives rise to impulses which excite new centres, the modality of which is a pain sensation so great as to cloak concomitant touch sensations.

However differences in nervous rhythm may account for minor differences in sensation, it remains clear that the characters of our sensations are creations of our own organism; they depend on properties of our Bodies and not on properties of external things, except in so far as these may or may not be adapted to arouse our different sensory apparatuses to activity. From the kind of the sensation we can-

not, therefore, argue as to the nature of the excitant: we have no more warrant for supposing that light is like our sensation of light than that the knife that cuts us is like our sensation of pain. All that we know with certainty is states of our own consciousness, and although from these we form working hypotheses as to an external universe, yet, granting it, we have no means of acquiring any real knowledge as to the properties of things about us. What we want to know, however, for the practical purposes of life is, not what things *are*, but how to use them for our advantage, or to prevent them from acting to our disadvantage; and our senses enable us to do this sufficiently well.

The Psycho-Physical Law. Although our sensations are, in modality or kind, independent of the force exciting them, they are not so in degree or intensity, at least within certain limits. We cannot measure the amount of a sensation and express it in foot-pounds or calories, but we can get a sort of unit by determining how small a difference in sensation can be perceived. Supposing this smallest perceptible difference to be constant within the range of the same sense (which is not proved), it is found that it is produced by different amounts of stimuli, measured objectively as forces; and that there exists in some cases a relation between the two which can be expressed in numbers. *The increase of stimulus necessary to produce the smallest perceptible change in a sensation is proportional to the strength of the stimulus already acting;* for example, the heavier a pressure already acting on the skin the more must it be increased or diminished in order that the increase or diminution may be felt. Expressed in another way the facts may be put thus: suppose three degrees of stimulation to bear to one another objectively the ratios 10, 100, 1000, then their subjective effects, or the amounts of sensation aroused by them, will be respectively as 1, 2, 3; in other words, *the sensation increases proportionately to the logarithm of the strength of the stimulus.* Examples of this, which is known as " *Weber's* " or " *Fechner's psycho-physical law* " will be hereafter pointed out, and are readily observable in daily life; we have, for example, a luminous sensation of certain intensity when a lighted candle is brought into a dark room; this sensation is not doubled when a second candle is brought in; and is hardly affected at all by a third. The law is only true, how-

ever (and then but approximately), for sensations of medium intensity; it is applicable, for example, to light sensations of all degrees between those aroused by the light of a candle and ordinary clear daylight: but it is not true for luminosities so feeble as only to be seen at all with difficulty, or so bright as to be dazzling.

Besides their variations in intensity, dependent on variations in the strength of the stimulus, our sensations also vary with the irritability of the sensory apparatus itself; which is not constant from time to time or from person to person. In the above statements the condition of the sense-organ and its nervous connections is presumed to remain the same throughout.

Perceptions. In every sensation we have to carefully distinguish between the pure sensation and certain judgments founded upon it; we have to distinguish between what we really feel and what we think we feel; and very often firmly believe we do feel when we do not.

The most important of these judgments is that which leads us to ascribe certain sensations, those aroused through organs of special sense, to external objects—that outer reference of our sensations which leads us to form ideas concerning the existence, form, position, and properties of external things. Such representations as these, founded on our senses, are called *perceptions.* Since these always imply some mental activity in addition to a mere feeling, their full discussion belongs to the domain of Psychology. Physiology, however, is concerned with them so far as it can determine the conditions of stimulation and neurosis under which a given mental representation concerning a sensation is made. It is quite certain that we can feel nothing but states of ourselves, but, as already pointed out, we have no hesitation in saying we feel a hard or a cold, a rough or smooth body. When we look at a distant object we usually make no demur to saying that we perceive it. What we really feel is, however, the change produced by it in our eyes. There are no parts of our Bodies reaching to a tree or a house a mile off— and yet we seem to feel all the while that we are looking at the tree or the house and feeling them, and not merely experiencing modifications of our own eyes or brains. When reading we *feel* that what we really see is the book; and yet

the existence of the book is a judgment founded on a state of our Body, which alone is what we truly feel.

We have the same experience in other cases, for example with regard to touch.

Hairs are quite insensible, but are imbedded in the sensitive skin, which is excited when they are moved. But if the tip of a hair be touched by some external object we believe we feel the contact at its insensible end, and not in the sensitive skin at its root. So, the hard parts of the teeth are insensible; yet when we rub them together we refer the seat of the sensation aroused to the points where they touch one another, and not to the sensitive parts around the sockets where the sensory nerve impulse is really started.

Still more, we may refer tactile sensations, not merely to the distal ends of insensible bodies implanted in the skin, but to the far ends of things which are not parts of our Bodies at all; for instance, the distant end of a rod held between the finger and a table while the finger is moved a little from side to side. We then believe we feel touch or pressure in two places; one where the rod touches our finger, and the other where it comes in contact with the table. A blind man gropes his way along by *feeling* at the end of his stick. If the rod is attached immovably to the table we feel only its end next the finger. If we could fix it immovably on the finger while the other end was movable on the table, we would lose the sensation at the finger and refer the sensation of pressure to where the rod touched the table. When a tooth is touched with a rod we only feel the contact at its end, unless it is loose in its socket; and then we get two sensations on touching its free end with a foreign body.

This irresistible mental tendency to refer certain of our states of feeling to causes outside of our Bodies, and either in contact with them or separated from them by a certain space, is known as the phenomenon of the *extrinsic reference of our sensations.* The discussion of its origin belongs properly to Psychology, and it will suffice here to point out that it seems largely to depend on the fact that the sensations extrinsically referred can be modified by movements of our Bodies. Hunger, thirst, and toothache all remain the same whether we turn to the right or left, or move away from the place we are standing in. But a sound is altered. We may find that in a certain position of the head it is heard more by the

right ear than the left; but on turning round the reverse is the case; and half way round the loudness in each ear is the same. Hence we are led, by mental laws outside of the physiological domain, to suspect that its cause is not in our Body, but outside of it; and depends not on a condition of the Body but on something else. And this is confirmed when going in one direction we find the sound increased, and in the other that it is diminished. This implies that we have a knowledge of our movements, and this we gain through the *muscular sense.* It constitutes the reactive side of our sensory life, associated with the changes we produce in external things; and is correlated and contrasted with the passive side, in which other things produce sensations by acting upon us.

As regards our common sensations we find something of the same kind. The more readily they can be modified by movement the more definitely do we localize them in space, though in this case within the Body instead of outside it. Hunger and nausea can be altered by pressure on the pit of the stomach; thirst by moistening the throat with water; the desire for oxygen (respiration-hunger) by movements of the chest; and so we more or less definitely ascribe these sensations to conditions of those parts of the Body. Other general sensations, as depression, anxiety, and so on, are not modifiable by any particular movement, and so appear to us rather as mental states, pure and simple, than bodily sensations.

Sensory Illusions. " I must believe my own eyes " and " we can't always believe our senses " are two expressions frequently heard, and each expressing a truth. No doubt a sensation in itself is an absolute incontrovertible fact: if I feel redness or hotness I do feel it, and that is an end of the matter: but if I go beyond the fact of my having a certain sensation and conclude from it as to properties of something else—if I form a *judgment* from my *sensation*—I may be totally wrong; and in so far be unable to believe my eyes or skin. Such judgments are almost inextricably woven up with many of our sensations, and so closely that we cannot readily separate the two; not even when we know that the judgment is erroneous.

For example, the moon when rising or setting appears bigger than when high in the heavens—we seem to feel

directly that it arouses more sensation, and yet we know certainly that it does not. With a body of a given brightness the amount of change produced in the end organs of the eye will depend on the size of the image formed in the eye, provided the same part of its sensory surface is acted upon. Now the size of this image depends on the distance of the object; it is smaller the farther off it is and greater the nearer, and measurements show that the area of the sensitive surface affected by the image of the rising moon is no larger than that affected by it when overhead. Why then do we, even after we know this, see it bigger? The reason is that when the moon is near the horizon we imagine, unconsciously and irresistibly, that it is farther off; even astronomers who know perfectly well that it is not, cannot help forming this unconscious and erroneous judgment—and to them the moon appears in consequence larger when near the horizon, just as it does to less well-informed mortals. In fact we have a conception of the sky over which the moon seems to travel, not as a half sphere but as somewhat flattened, and hence when the moon is at the horizon we unconsciously judge that it is farther off than when overhead. But any body which excites the same extent of the sensitive surface of the eye at a great distance that another does at less, must be larger than the latter; and so we conclude that the moon at the horizon is larger than the moon in the zenith, and are ready to declare that we see it so.

So, again, a small bit of pale gray paper on a white sheet looks gray: but placed on a large bright green surface it looks purple; and on a bright red surface looks blue-green. As the same bit of gray paper is shifted from one to the other we see it change its color: it arouses in us different feelings, or feelings which we interpret differently, although objectively the light reflected from it remains the same. Similarly a medium-sized man alongside of a very tall one appears short, but when walking with a very short one, tall.

Such erroneous perceptions as these are known as *sensory illusions;* and we ought to be constantly on guard against them.

CHAPTER XXXII.

THE EYE AS AN OPTICAL INSTRUMENT.

The Essential Structure of an Eye. Every visual organ consists primarily of a nervous expansion, provided with end-organs by means of which light is enabled to excite nervous impulses, and exposed to the access of objective light; such an expansion is called a *retina*. By itself, however, a retina would give no visual sensations referable to distinctly limited external objects; it would enable its possessor to tell light from darkness, more light from less light, and (at least in its highly developed forms) light of one color from light of another color; but that would be all. Were our eyes merely retinas we could only tell a printed page from a blank one by the fact that, being partly covered with black letters (which reflect less light), it would excite our visual organ less powerfully than the spotless white page would. In order that distinct objects and not merely degrees of luminosity may be seen, some arrangement is needed which shall bring all light entering the eye from one point of a luminous surface to a *focus* again on one point of the sensitive surface. If A and B (Fig. 139) be two red spots on a black surface, K, and rr be a retina, then rays of light diverging from A would fall equally on all parts of the retina and excite it all a little; so with rays starting from B. The sensation aroused, supposing the retina in connection with the rest of the nervous visual apparatus, would be one of a certain amount of red light reaching the eye; the red spots, as definite objects, would be indistinguishable. If, however, a convex glass lens L (Fig. 140) be put in front of the retina, it will cause to converge again to a single point all the rays from A falling upon it; so, too, with the rays from B : and if the focal distance of the lens be properly adjusted these points of convergence will both lie on the retina, that for rays from A at a, and that for rays from B at b. The sensitive surface would then only be excited at two limited and separated points by

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the red light emanating from the spots; consequently only some of its end-organs and nerve-fibres would be stimulated and the result would be the recognition of two separate red
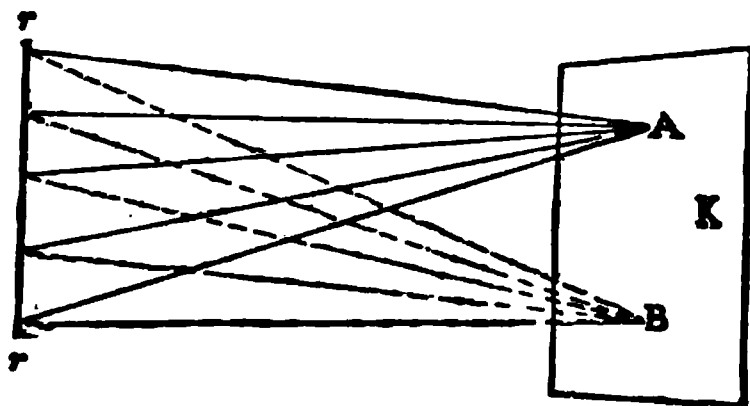
Fig. 189.—Diagram illustrating the indistinctness of vision with a retina alone. *K*, a surface on which are two spots, *A* and *B*; *r r*, the retina. The diverging lines represent rays of light spread uniformly over the retina from each spot.

objects. In our eyes there are certain *refracting media* which lie in front of the retina and take the place of the lens *L* in Fig. 140. That portion of physiology which treats of
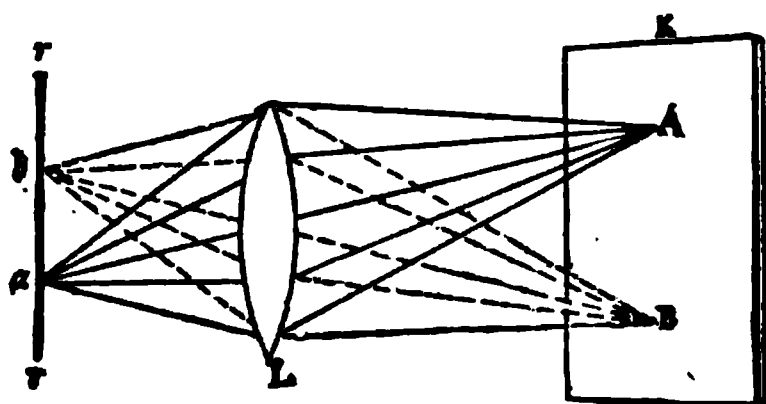
Fig. 140.—Illustrating the use of a lens in giving definite retinal images. *A*, *B*, *K*, *r r*, as in Fig. 189. *L*, a biconvex lens so placed that it brings to a focus on the points *a* and *b* of the retina, rays of light diverging from *A* and *B* respectively.

the physical action of these media or, in other words, of the eye as an optical instrument, is known as the *dioptrics* of the eye.

The Appendages of the Eye. The eyeball itself consists of the retina and refracting media, together with supporting and nutritive structures and other accessory apparatuses, as, for example, some controlling the light-converging power of the media, and others regulating the size of the aperture (*pupil*) by which light enters. Outside the ball lie muscles which bring about its movements, and other parts serving to protect it.

Each orbit is a pyramidal cavity occupied by connective tissue, muscles, blood-vessels and nerves, and in great part by fat, which forms a soft cushion on which the back of the eyeball lies and rolls during its movements. The contents of .

the orbit being for the most part incompressible, the eye can-not be drawn into its socket. It simply rotates there, as the head of the femur does in the acetabulum. When the orbital blood-vessels are gorged, however, the eyeball may protrude (as in strangulation); and when these vessels empty it recedes somewhat, as is commonly seen after death. The front of the eye is exposed for the purpose of allowing light to reach it, but can be covered up by the *eyelids*, which are folds of integument, movable by muscles and strengthened by plates of fibro-cartilage. At the edge of each eyelid the skin which covers its outside is turned in, and becomes continuous with a mucous membrane, the *conjunctiva*, which lines the inside of each lid, and also covers all the front of the eyeball as a closely adherent layer.

The upper eyelid is larger and more mobile than the lower, and when the eye is closed covers all its transparent part. It has a special muscle to raise it, the *levator palpebræ superioris*. The eyes are closed by a flat circular muscle, the *orbicularis palpebrarum* which, lying on and around the lids, immediately beneath the skin, surrounds the aperture between them. At their outer and inner angles (*canthi*) the eyelids are united, and the apparent size of the eye depends upon the interval between the canthi, the eyeball itself being nearly of the same size in all persons. Near the inner canthus the line of the edge of each eyelid changes its direction and becomes more horizontal. At this point is found a small eminence, the *lachrymal papilla*, on each lid. For most of their extent the inner surfaces of the eyelids are in contact with the outside of the eyeball, but near their inner ends a red vertical fold of conjunctiva, the *semilunar fold* (*plica semilunaris*) intervenes. This is a representative of the third eyelid, or *nictitating membrane,* found largely developed in many animals, as birds, in which it can be drawn all over the exposed part of the eyeball. At the inner or nasal corner is a reddish elevation, the *caruncula lachrymalis,* caused by a collection of sebaceous glands imbedded in the semilunar fold. Opening along the edge of each eyelid are from twenty to thirty minute compound sebaceous glands, named the Meibomian follicles. Their secretion is sometimes abnormally abundant, and then appears as a yellowish matter along the edges of the eyelids, which often dries in the night and causes the lids to be glued together in the morning.

The *eyelashes* are short curved hairs, arranged in one or two rows along each lid where the skin joins the conjunctiva.

The Lachrymal Apparatus consists of the tear-gland in each orbit, the ducts which carry its secretion to the upper eyelid, and the canals by which the tears, unless when excessive, are carried off from the front of the eye without running down over the face. The *lachrymal* or *tear gland*, about the size of an almond, lies in the upper and outer part of the orbit, near the front end. It is a compound racemose gland, from which twelve or fourteen ducts run and open in a row at the outer corner of the upper eyelid. The secretion there poured out, is spread evenly over the exposed part of the eye by the movements of winking, and keeps it moist; finally the tear is drained off by two *lachrymal canals*, one of which opens by a small pore (*punctum lachrymalis*) on each lachrymal papilla. The aperture of the lower canal can be readily seen by examining the corresponding papilla by the aid of a looking-glass. The canals run inwards and open into the *lachrymal sac*, which lies just outside the nose, in a hollow where the lachrymal and superior maxillary bones (*L* and *Mx*, Fig. 30) meet. From the sac the *nasal duct* proceeds to open into the nose-chamber, below the inferior turbinate bone and within the nostril.

Tears are constantly being secreted, but ordinarily in such quantity as to be drained off into the nose, from which they flow into the pharynx and are swallowed. When the lachrymal ducts are stopped up, however, their continual presence makes itself unpleasantly felt, and may need the aid of a surgeon to clear the passage. In *weeping* the secretion is increased, and then not only more of it enters the nose, but some flows down the cheeks. The frequent swallowing movements of a crying child, sometimes spoken of as " gulping down his passion," are due to the need of swallowing the extra tears which reach the pharynx.

The Muscles of the Eye (Fig. 141). The eyeball is spheroidal in form and attached behind to the optic nerve, *n*, somewhat as a cherry might be to a thick stalk. On its exterior are inserted the tendons of six muscles, four *straight* and two *oblique*. The straight muscles lie, one (*superior rectus*), *s*, above, one (*inferior rectus*) below, one (*external rectus*), *a*, outside, and one (*internal rectus*), *i*, inside the eyeball. Each arises behind from the bony margin of the

foramen through which the optic nerve enters the orbit. In the figure, which represents the orbits opened from above, the superior rectus of the right side has been removed. The *superior oblique* or *pulley (trochlear) muscle, t,* arises behind near the straight muscles and forms anteriorly a tendon, *u,* which passes through a fibro-cartilaginous ring, or pulley, placed at the notch in the frontal bone where it bounds superiorly the front end of the orbit. The tendon then turns

Fig. 141.—The eyeballs and their muscles as seen when the roof of the orbit has been removed and the fat in the cavity has been partly cleared away. On the right side the superior rectus muscle has been cut away. *a,* external rectus, *s,* superior rectus ; *i,* internal rectus; *t,* superior oblique.

back and is inserted into the eyeball between the upper and outer recti muscles. The *inferior oblique muscle* does not arise, like the rest, at the back of the orbit, but near its front at the inner side, close to the lachrymal sac. It passes thence outwards and backwards beneath the eyeball to be inserted into its outer and posterior part.

The inner, upper, and lower straight muscles, the inferior oblique, and the elevator of the upper lid are supplied by branches of the third cranial nerve. The sixth cranial nerve goes to the outer rectus; and the fourth to the superior oblique.

The eye may be moved from side to side; up or down; obliquely, that is neither truly vertically nor horizontally, but partly both; or, finally, it may be rotated on its antero-posterior axis. The oblique movements are always accom-

panied by a slight amount of rotation. When the glance is turned to the left, the left external rectus and the right internal contract, and *vice versa;* when up, both superior recti; when down, both the inferior. The superior oblique muscle acting alone will roll the front of the eye downwards and outwards with a certain amount of rotation; the inferior oblique does the reverse. In oblique movements two of the recti are concerned, an upper or lower with an inner or outer; at the same time one of the oblique also always contracts. Movements of rotation rarely, if ever, occur alone.

The natural combined movements of the eyes by which both are directed simultaneously towards the same point depends on the accurate adjustment of all its nervo-muscular apparatus. When the co-ordination is deficient the person is said to *squint.* A left *external squint* would be caused by paralysis of the inner rectus of that eye, for then, after the eyeball had been turned out by the external rectus, it would not be brought back again to its median position. A left *internal squint* would be caused, similarly, by paralysis of the left external rectus; and probably by disease of the sixth cranial nerve or its brain-centres. Dropping of the upper eyelid (*ptosis*) indicates paralysis of its special elevator muscle and is often a serious symptom, pointing to disease of the brain-parts from which it is innervated.

The Globe of the Eye is on the whole spherical, but consists of segments of two spheres (see Fig. 142), a portion of a sphere of smaller radius forming its anterior transparent part and being set on to the front of its posterior segment, which is part of a larger sphere. From before back it measures about 22.5 millimeters ($\frac{9}{10}$ inch), and from side to side about 25 millimeters (1 inch). Except when looking at near objects, the antero-posterior axes of the eyeballs are nearly parallel, though the optic nerves diverge considerably (Fig. 141); each nerve joins its eyeball, not at the centre, but about 2.5 mm. ($\frac{1}{10}$ inch) on the nasal side of the posterior end of its antero-posterior axis. In general terms the eyeball may be described as consisting of three *coats* and three *refracting media.*

The outer coat, 1 and 3, Fig. 142, consists of the *sclerotic* and the *cornea,* the latter being transparent and situated in front; the former is opaque and white and covers the back and sides of the globe and part of the front, where it is seen

between the eyelids as the *white* of the eye. Both are tough and strong, being composed of dense connective tissue. The white of the eye and the cornea are covered by a thin layer of the conjunctiva, 4 and 5. Behind the proper connective-tissue layer, 3, of the cornea is a thin structureless membrane,
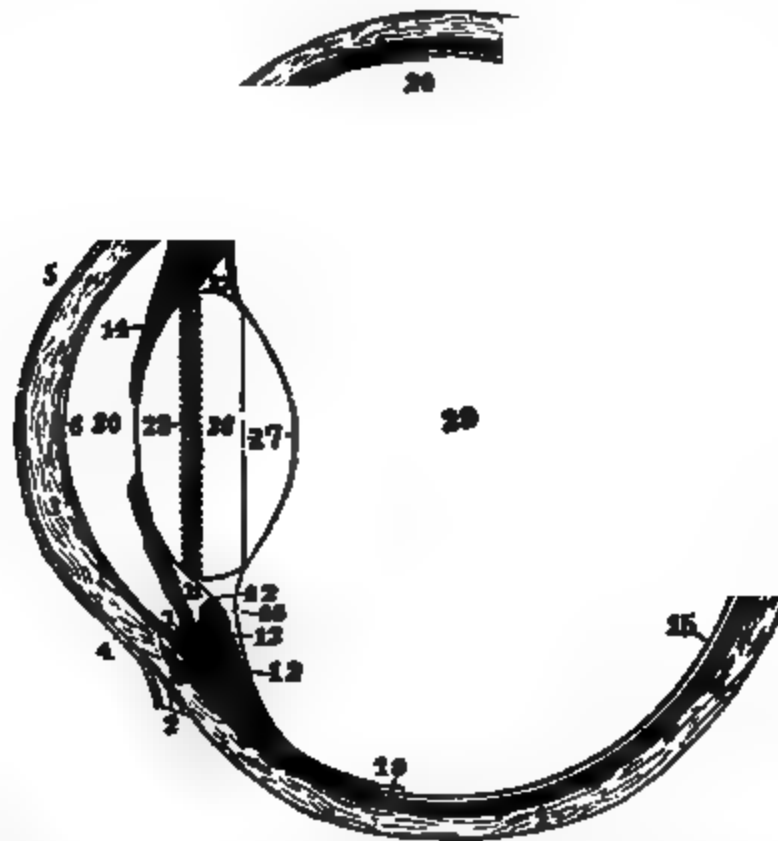
Fig. 147.—The left eyeball in horizontal section from before back. 1, sclerotic; 2, junction of sclerotic and cornea; 3, cornea; 4, 5, conjunctiva; 6, posterior elastic layer of cornea; 7 ciliary muscle; 10, choroid; 11, 13, ciliary processes; 14, iris; 15, retina; 16, optic nerve; 17, artery entering retina in optic nerve; 18, fovea centralis; 19, region where sensory part of retina ends; 22, suspensory ligament; 23 is placed in the canal of Petit and the line from 25 points to it; 24, the anterior part of the hyaloid membrane; 26, 27, 28 are placed on the lens; 25 points to the line of attachment around it of the suspensory ligament; 29, vitreous humor; 30, anterior chamber of aqueous humor; 31, posterior chamber of aqueous humor.

6, lined inside by a single layer of epithelial cells; it is the *membrane of Descemet*, or the *posterior elastic layer*.

The second coat consists of the *choroid*, 9, 10, the *ciliary processes*, 11, 13, and the *iris*, 14. The *choroid* is made up of blood-vessels supported by loose connective tissue containing numerous corpuscles, which in its inner layers are richly filled with dark-brown or black pigment granules. Towards the front of the eyeball, where it begins to diminish in diameter, the choroid is thrown into plaits, the *ciliary processes*, 11, 13. Beyond these it continues as the *iris*, which forms the colored part of the eye seen through the cornea; and in the centre of the iris is a circular aperture,

the *pupil:* so its second coat does not, like the outer one, completely envelop the eyeball. In the iris is a ring of plain muscular tissue encircling the aperture of the pupil: when its fibres contract they narrow the pupil. Radial fibres can be found passing from the ring to the outer edge of the iris, and they have been supposed to be muscular and concerned in dilating the pupil. They are probably merely elastic and, being stretched when the circular muscle contracts, by mere physical elasticity dilate the pupil when the muscle relaxes. The circular or sphincter muscle appears to be normally in a state of tonic contraction; this is increased by impulses travelling in fibres of the third cranial nerve and is diminished or inhibited by impulses travelling along fibres of the sympathetic, which, however, have their origin in the medulla oblongata and run down the spinal cord to the lower part of the neck, where they pass out in anterior spinal nerve-roots to reach the sympathetic. The pigment in the iris is yellow, or of lighter or darker brown, according to the color of the eye, and more or less abundant according as the eye is black, brown, or gray. In blue eyes the pigment is confined to the deeper layers, and modified in tint by light absorption in the anterior colorless strata through which the light passes.

The third coat of the eye, *the retina,* 15, is its essential portion, being the part in which the light produces those changes that give rise to impulses in the optic nerve. It is a still less complete envelope than the second tunic, extending forwards only as far as the commencement of the ciliary processes, at least in its typical form. It is extremely soft and delicate; and, when fresh, transparent. Usually when an eye is opened the retina is colorless; but when the eye has been cut open in faint yellow light and the exposed retina quickly examined in white light it is seen to be purple. The coloring substance (*visual purple*) very rapidly bleaches when a dead eye is exposed to daylight. On front or inner surface of the human retina two special areas can be distinguished in a fresh eye. One is the point of entry of the optic nerve, 16, the fibres of which, penetrating the sclerotic and choroid, spread out in the retina. At this place the retina is whiter than elsewhere and presents an elevation, the *optic mound.* The other peculiar region is the *yellow spot* (*macula lutea*), 18, which lies nearly at the posterior end of the axis of the eye.

ball and therefore outside the optic mound; in its centre the retina is thinner than elsewhere and so a pit (*fovea centralis*), 18, is formed. This appears black, the thinned retina there allowing the choroid to be seen through it more clearly than elsewhere. In Fig. 143 is represented the left retina as seen from the front, the elliptical darker patch about the centre indicating the yellow spot, and the white circle on one side, the optic mound. The vessels of the retina arise from an artery (17, Fig. 142) which runs in with the optic nerve and from which branches diverge as shown in Fig. 143.

The Optic Nerves, Commissure, and Tracts. The optic nerves converge to meet in the optic commissure (*m*, Fig. 141), from which the optic tracts pass to the region of the midbrain. They terminate mainly in the anterior corpora quadrigemina (Chap. XII) and in masses of gray nerve matter lying to the outer sides and in front of these, and known as the corpora geniculata. At the commissure (*m*, Fig. 141) many fibres cross the middle line, so that fibres from each optic nerve are found in both optic tracts. In general, fibres from the right (that is, the outer or temporal) side of the right retina and the right (*i.e.* nasal) side of the left retina pass on to the brain in the right optic tract; and similarly for the left sides of the two retinas. Cutting the right optic nerve, therefore, causes total blindness of the right eye, but cutting of the right optic tract blindness of the right half of each retina (*hemianopia*). It will later be seen that rays of light cross in the eye so that objects to the left in space form images on the right sides of the retinas; and *vice versa* (Figs. 153, 154). Consequently section or extensive disease of the right optic tract causes *left hemianopia;* that is, blindness to objects on the left of the line of vision.

The incomplete crossing of the optic nerve-fibres in man is correlated with the fact that his eyes are so placed that part of the field of vision is common to both. In mammals whose eyes are so laterally placed that at any given moment the objects seen by the two eyes are quite different, the crossing at the commissure is complete; when the eyes are placed so that some objects can be seen simultaneously by the two eyes, some fibres cross, and a greater number cross the larger, the common part of the visual fields. Even in man more of the fibres cross than go direct to the same side of the brain.

The Microscopic Structure of the Retina. A simplified stratum, continuous with the proper retina, and formed of a layer of nucleated columnar cells, is continued over the ciliary processes; elsewhere the membrane has a very complex structure, and a section taken, except at the yellow spot or the optic mound, shows ten layers, partly sensory apparatuses and nerve-tissues, and partly accessory structures.

Beginning (Fig. 144) on the front side we find, first, the *internal limiting membrane*, 1, a thin structureless layer. Next comes the *nerve-fibre layer*, 2, formed by radiating fibres of the optic nerve; third, the *nerve-cell layer*, 3; fourth,

$$\frac{5}{1}$$

Fig. 144.—The right retina as it would be seen if the front part of the eyeball with the lens and vitreous humor were removed.

the *inner molecular layer*, 4, consisting partly of very fine nerve-fibrils, and largely of connective tissue; fifth, the *inner nuclear layer*, 5, composed of nucleated cells, with a small amount of protoplasm at each end, and a nucleolus. These cells, or at any rate the majority of them, have an *inner process* running to the inner molecular layer and an outer running to, 6, the *outer molecular layer*, which is thinner than the inner. Then comes, seventh, the *rod and cone fibre layer*, 7, or outer nuclear layer; composed of thick and thin fibres in each of which is a conspicuous nucleus with a nucleolus. Next is the thin *external limiting membrane*, 8, perforated by apertures through which the *rods and cones*, 9, of the ninth layer join the fibres of the seventh. Outside of all, next the choroid, is the *pigmentary layer*, 10;

the cells of this layer send processes between the rods and
cones. The processes contain dark pigment and in eyes
which have been exposed to bright light reach a long way,
sometimes even as far as the external limiting membrane.
If, however, the animal have been kept in the dark for some

Fig. 144.—A section through the retina from its anterior or inner surface, 1, in
contact with the hyaloid membrane, to its outer, 10, in contact with the choroid.
1, internal limiting membrane. 2. nerve-fibre layer; 3, nerve-cell layer; 4, inner
molecular layer; 5, inner nuclear layer; 6, outer molecular layer; 7, rod and cone
fibres or outer nuclear layer; 8, external limiting membrane; 9, rod and cone
layer; 10, pigment-cell layer

time before its eye is removed, the processes of the pigment-
cells are short and extend only a short distance between the
outer ends of the rods. In addition, certain fibres run verti-
cally through the retina from the inner to the outer limiting
membrane; they are known as the *radial fibres of Müller*

and give off lateral branches, which are especially numerous in the molecular layers. Like the limiting membranes they are merely supporting tissues.

On account of the way in which the supporting and essential parts are interwoven in the retina it is not easy to track the latter through it. There is, however (Chap. XXXIII), good evidence that light first acts upon the rod and cone layer, traversing all the thickness of inner strata of the retina to reach it, before starting those changes which result in visual sensations; and it is therefore probable that the rods and cones are in direct continuity with the optic nerve-fibres. The limiting membranes, with the fibres of Müller and their branches, are undoubtedly merely accessory and supporting.

Each rod and cone consists of an *outer* and an *inner segment*. The outer segments of both tend to split up transversely into disks and are very similar, except that those of the rods are longer than those of the cones and do not taper as the latter do. Moreover, the visual purple is entirely confined to the outer segments of the rods, the cones containing none of it. The inner segments of the cones are swollen, while those of the rods are narrow and nearly cylindrical. Over most of the retina the rods are longer and much more numerous than the cones, but near the ciliary processes they cease before the cones do; and in the yellow spot elongated cones alone are found. In this region the whole retina is modified; at its margin all the layers are thickened but especially the nerve-cell layer, which becomes six or seven thick, while elsewhere the cells are found in but one or two strata. Most of the fibres run obliquely, reaching in to become continuous with the cones of the central pit, which are long, slender, and very closely packed. In the fovea itself all the layers, except that of the cones, thin away, and thus the depression is produced. The fovea is the seat of most acute vision; when we look at an object we always turn our eyes so that the light proceeding from it shall be focussed on the two foveæ. Where the optic nerve enters, all the layers but the nerve-fibre layer (which is there very thick), and the internal limiting membrane, are absent.

The blood-vessels of the retina lie almost entirely in the nerve-fibre and nerve-cell layers.

The **Refracting Media of the Eye** are, in succession from before back, the *cornea*, the *aqueous humor*, the *crystalline lens*, and the *vitreous humor*.

The *aqueous humor* fills the space between the front of the lens, 28, and the back of the cornea. This space is incompletely divided by the iris into an anterior chamber, 30, and a posterior, 31 (Fig. 142). Chemically, the aqueous humor consists of water holding in solution a small amount of solid matters, mainly common salt.

The *crystalline lens* (28, 26, 27) is colorless, transparent, and biconvex, with its anterior surface less curved than the posterior. It is surrounded by a capsule, and the inner edge of the iris lies in contact with it in front. In consistence it is soft, but its central layers are rather more dense than the outer.

The *vitreous humor* is a soft jelly enveloped in a thin capsule, the *hyaloid membrane.* In front, this membrane splits into two layers, one of which, 22, passes on to be fixed to the lens a little in front of its edge. This layer is known as the *suspensory ligament of the lens;* its line of attachment around that organ is not straight but sinuous as represented by the curved line between 28 and 26 in Fig. 142. The space between the two layers into which the hyaloid splits is the *canal of Petit.* The vitreous humor consists mainly of water and contains some salts, a little albumin, and some mucin. It is divided up, by delicate membranes, into compartments in which its more liquid portions are imprisoned.

The Ciliary Muscle. Running around the eyeball where the cornea joins the sclerotic is a lymph-vessel called the *canal of Schlemm;* it is seen in section at 8 in Fig. 142. Lying on the inner side of this canal, just where the iris and the ciliary processes meet, there is some plain muscular tissue, imbedded mainly in the middle coat of the eyeball and forming the *ciliary muscle,* which consists of a *radial* and a *circular* portion (Fig. 149). The radial part is much the larger, and arises in front from the inner surface of the sclerotic; the fibres pass back, spreading out as they go, and are inserted into the front of the choroid opposite the ciliary processes. The circular part of the muscle lies around the outer rim of the iris. The contraction of the ciliary muscle tends to pull forward (radial fibres) and press inward (circular fibres) the front part of the choroid, to which the back part of the suspensory ligament of the lens is closely attached. · When this occurs the tension exerted on the margin of the lens by its ligament is diminished.

The Properties of Light. Before proceeding to the

study of the eye as an optical instrument, it is necessary to recall briefly certain properties of light.

Light is considered as a form of movement of the particles of an hypothetical medium, or ether, the vibrations being in planes at right angles to the line of propagation of the light. When a stone is thrown into a pond a series of circular waves travel from that point in a *horizontal direction* over the water, while the particles of water themselves move *up and down*, and cause the surface inequalities which we see as the waves. Somewhat similarly, light-waves spread out from a luminous point, but in the same medium travel equally in all directions so that the point is surrounded by shells of spherical waves, instead of rings of circular waves travelling in one plane only, as those on the surface of the water. Starting from a luminous point light would travel in all directions along the radii of a sphere of which the point is the centre; the light propagated along one such radius is called a *ray*, and in each ray the ethereal particles swing from side to side in a plane perpendicular to the direction of the ray. Taking a particle on any ray it would swing aside a certain distance from it, then back to it again, and across for a certain distance on the other side; and then back to its original position on the line of the ray. Such a movement is an *oscillation*, and takes a certain time; in lights of certain kinds the *periods of oscillation* are all the same, no matter how great the extent or *amplitude* of the oscillation; just as a given pendulum will always complete its swing in the same time no matter whether its swings be great or small. Light composed of rays in which the periods of oscillation are all equal is called *monochromatic* or *simple light,* while light made of a mixture of oscillations of different periods is called *mixed* or *compound light.*

If monochromatic light is steadily emitted from a point, we come at definite distances along a ray, to particles in the same *phase* of oscillation, say at their greatest distance from their position of rest; just as in the concentric waves seen on the water after throwing in a stone we would along any radius meet, at intervals, with water raised most above its horizontal plane as the *crest* of a wave, or depressed most below it as the *hollow* of a wave. The distance along the ray from crest to crest is called a *wave-length* and is always the same in any given simple light; but it is different in simple

lights of different colors; the briefer the time of an oscillation the less the wave-length.

When light falls on a polished surface separating two transparent media, as air and glass, part of it is *reflected* or turned back into the first medium; part goes on into the second medium, and is commonly deviated from its original course or *refracted*. The original ray falling on the surface is the *incident* ray.
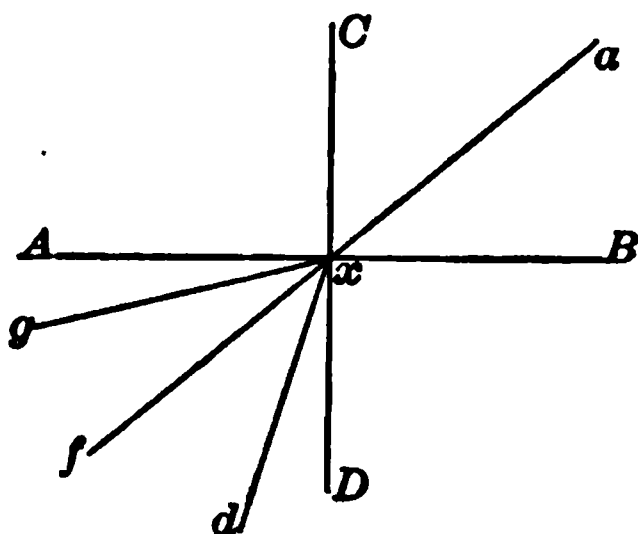
FIG. 145.—Diagram illustrating the refraction of light. *A B*, surface of separation between two transparent media; *C D*, the perpendicular to the surface at the point of incidence. *x*; *a x*, incident ray; *x d*, refracted ray, if the second medium be denser than the first; *x g*, refracted ray, if the second medium is less refractive than the first. The reflected ray is not represented, but would make an angle with *C x*, equal to the angle *a x C*.

Let *A B* (Fig. 145) be the surface of separation; *a x* the incident ray; and *C D* the perpendicular or normal to the surface at the point of incidence: *a x C* will then be the *angle of incidence*. Then the reflected ray makes an *angle of reflection* with the normal which is equal to the angle of incidence; and the reflected ray lies in the same plane as the incident ray and the normal to the surface at *x*. The refracted ray lies also in the same plane as the normal and the incident ray, but does not continue in its original direction, *x f*; if the medium below *A B* be more refractive than that above it, the refracted ray is bent, as *x d*, nearer to the normal, and making with it an *angle of refraction*, *D x d*, smaller than the angle of incidence, *a x C*. If, on the contrary, the second medium is less refracting than the first, the refracted ray *x g* is bent away from the normal, and makes an angle of refraction, *D x g*, greater than the angle of incidence. The ratio of the sine of the angle of incidence to that of the angle of refraction is always the same for the same two media with light of the same wave-length. When the first medium is air the ratio of the sine of the angle of refraction to that of the angle of incidence is called the refractive index of the second medium. The greater this refractive index the more is the refracted ray deviated from its original course. Rays which fall perpendicularly on the surface of separation of two media pass on without refraction.

The shorter the oscillation periods of light-rays the more they are deviated by refraction. Hence mixed light when
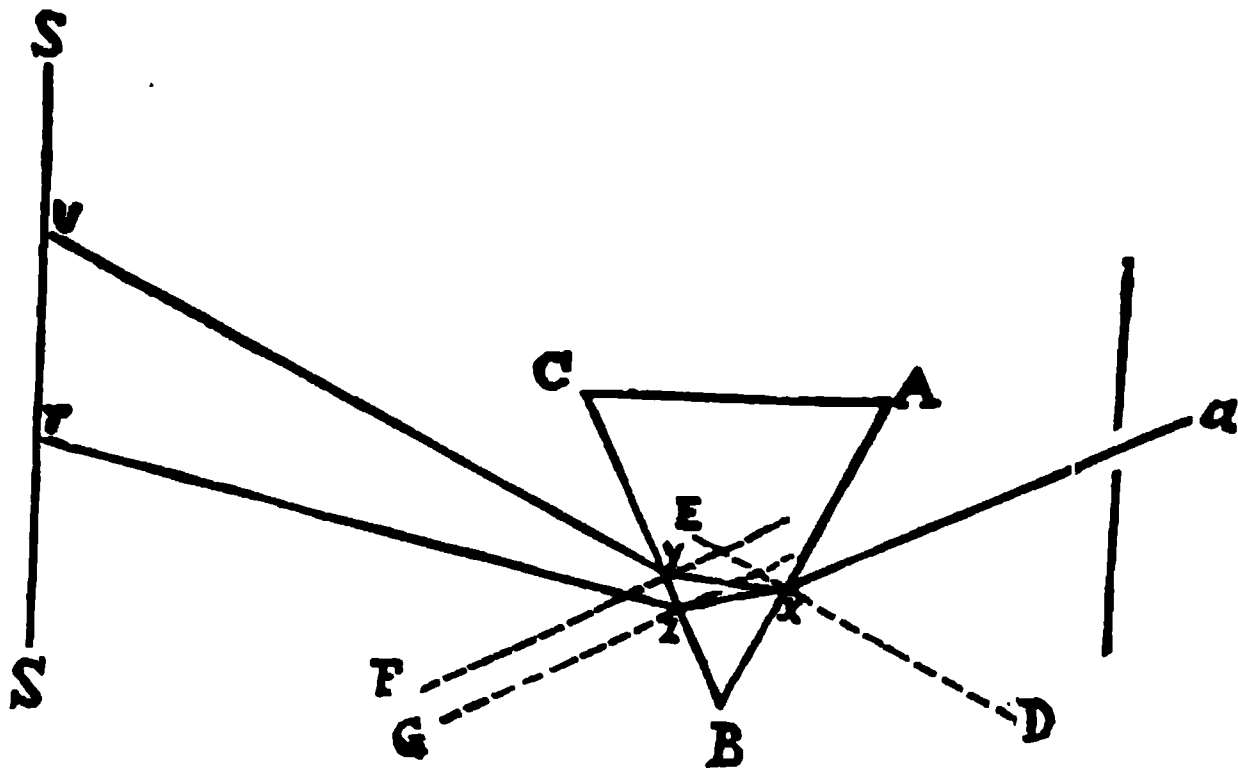
Fig. 146.—Diagram illustrating the dispersion of mixed light by a prism.

sent through a prism is spread out, and decomposed into its simple constituents. For let *a x* (Fig. 146) be a ray of mixed light composed of a set of short and a set of long ethereal waves. When it falls on the surface *A B* of the prism, that portion which enters will be refracted towards the normal *E D*, but the short waves more than the longer. Hence the former will take the direction *x y*, and the latter the direction *x z*. On emerging from the prism both rays will again be refracted, but now from the normals *F y* and *G z*, since the light is passing from a more to a less refracting medium. Again the ray *x y*, made up of shorter waves, will be most deviated, as in the direction *y v*, and the long waves less, in the direction *z r*. If a screen were put at *S S'*, we would receive on it at separate points, *v* and *r*, the two simple lights which were mixed together in the compound incident ray *a x*. Such a separation of light-rays is called *dispersion*.

Ordinary white light, such as that of the sun, is composed of ethereal vibrations of every rate, mixed together. When such light is sent through a prism it gives a continuous band of light-rays, known as the *solar spectrum*, reaching from the least refracted to the most refracted and shortest waves. The exceptions to this statement due to Frauenhofer's lines (see Physics) are unessential for our present purpose. All of the simple lights into which the compound solar light is thus

separated do not, however, excite in us visual sensations when they fall into the eye, but only certain middle ones. If solar light were used with the prism, Fig. 146, certain least refracted rays between *r* and *S'* would not be seen, nor the most refracted between *v* and *S*; while between *v* and *r* would stretch a luminous band exciting in us the series of color sensations from red (due to the least refracted visible rays), through orange, yellow, green, bright blue, and indigo, to violet, which latter is the sensation aroused by the most refrangible visible rays. The still shorter waves beyond the violet can only be seen under special conditions; they are known mainly by their chemical effects and are called the *actinic rays;* the invisible waves beyond the red exert a powerful heating influence and compose. the *dark-heat* rays. The eye, as an organ for making known to us the existence of ethereal vibrations, has, therefore, only a limited range.

Refraction of Light by Lenses. In the eye the refracting media have the form of lenses thicker in the centre than towards the periphery; and we may here confine ourselves therefore to such *converging lenses.* If simple light from a point *A*, Fig. 140, fall on such a lens its rays, emerging on the other side, will take new directions after refraction and meet anew at a point, *a*, after which they again diverge. If a screen, *r r*, be held at *a* it will therefore receive an image of the luminous point *A*. For every converging lens there is such a point behind it at which the rays from a given point in front of it meet: the point of meeting is called the *conjugate focus* of the point from which the rays start. If instead of a luminous point a luminous object be placed in front of the lens an image of the object will be formed at a certain distance behind it, for all rays proceeding from one point of the object will meet in the conjugate focus of that point behind. The image is inverted, as can be readily seen from

Fig. 147. All rays from the point *A* of the object meet at the point *a* of the image; those from *B* at *b*, and those from intermediate points at intermediate positions. If the single lens were replaced by several combined so as to form an
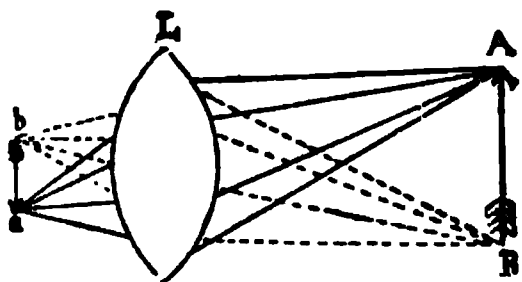
Fig. 147.—Diagram illustrating the formation of an image by a converging lens.

optical system the general result would be the same, provided the system were thicker in the centre than at the periphery.

The Camera Obscura, as used by photographers, is an instrument which serves to illustrate the formation of images by converging systems of lenses It consists of a box blackened inside and naving on its front face a tube containing the lenses; the posterior wall is made of ground glass. If the front of the instrument be directed on exterior objects, inverted and diminished images of them will be formed on the ground glass; those images only are well defined, at any one time, which are at such a distance in front of the instrument that the conjugate foci of points on them fall exactly on the glass behind the lens: objects nearer or farther off give confused and indistinct images; but by altering the distance between the lenses and the ground glass, in common language "focussing the instrument," either can be made distinct. For near objects the lenses must be farther from the surface on which the image is to be received, and for distant nearer. The reason of this may readily be seen from Fig. 148. If the system of lenses brings the parallel rays $a\,c$ and $b\,d$, proceeding from an infinitely distant object, to a focus at x, then the diverging rays $f\,c$ and $f\,d$, proceeding from a nearer point, will be harder to bend round, so to speak, and will not meet until a point y, farther behind the system than x is. The more divergent the rays, or what amounts to the same thing, the nearer the point they proceed from, the farther behind the refracting system will y be.
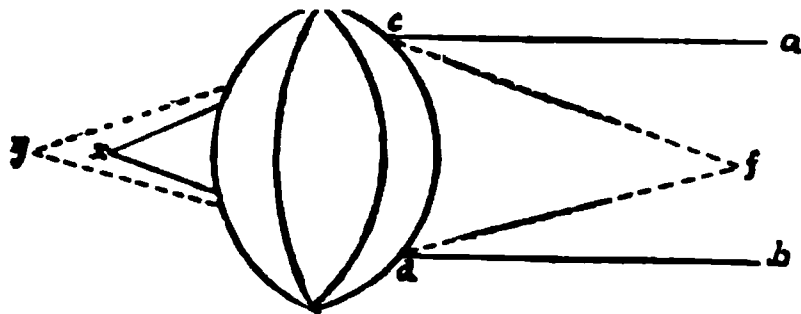
The refracting media of the eye form a convergent optical system, made up of cornea, aqueous humor, lens, and vitreous humor. These four media are reduced to three practically, by the fact that the indices of refraction of the cornea and aqueous humor are the same, so that they act together as one converging lens. The surfaces at which refraction occurs are—(1) that between the air and the cornea, (2) that between the aqueous humor and the front of the lens, (3) that between the vitreous humor and the back of the lens. The refractive

indices of those media are—the air, 1; the aqueous humor, 1.3379; the lens (average), 1.4545; the vitreous humor, 1.3379. From the laws of the refraction of light it therefore follows that (Fig. 149) the rays *C d* will at the corneal surface be refracted towards the normals *N*, *N*, and take the course *d e.* At the front of the lens they will again be refracted towards the normals to that surface and take the course *e f;* at the back of the lens, passing from a more refracting to a less refracting medium, they will be bent from the normals *N"* and take the course *f g.* If the retina be there, these parallel rays will therefore be brought to a focus on it. In the resting condition of the natural eye this is what happens to parallel rays entering it: and, since distant objects send into the eye rays which are practically parallel, such objects are seen distinctly without any effort, because all rays emanating from a point of the object meet again in one point on the retina.

Accommodation. Points on near objects send into the eye diverging rays: these therefore would not come to a focus on the retina but behind it, and would not be seen distinctly, did not some change occur in the eye; since we can see them
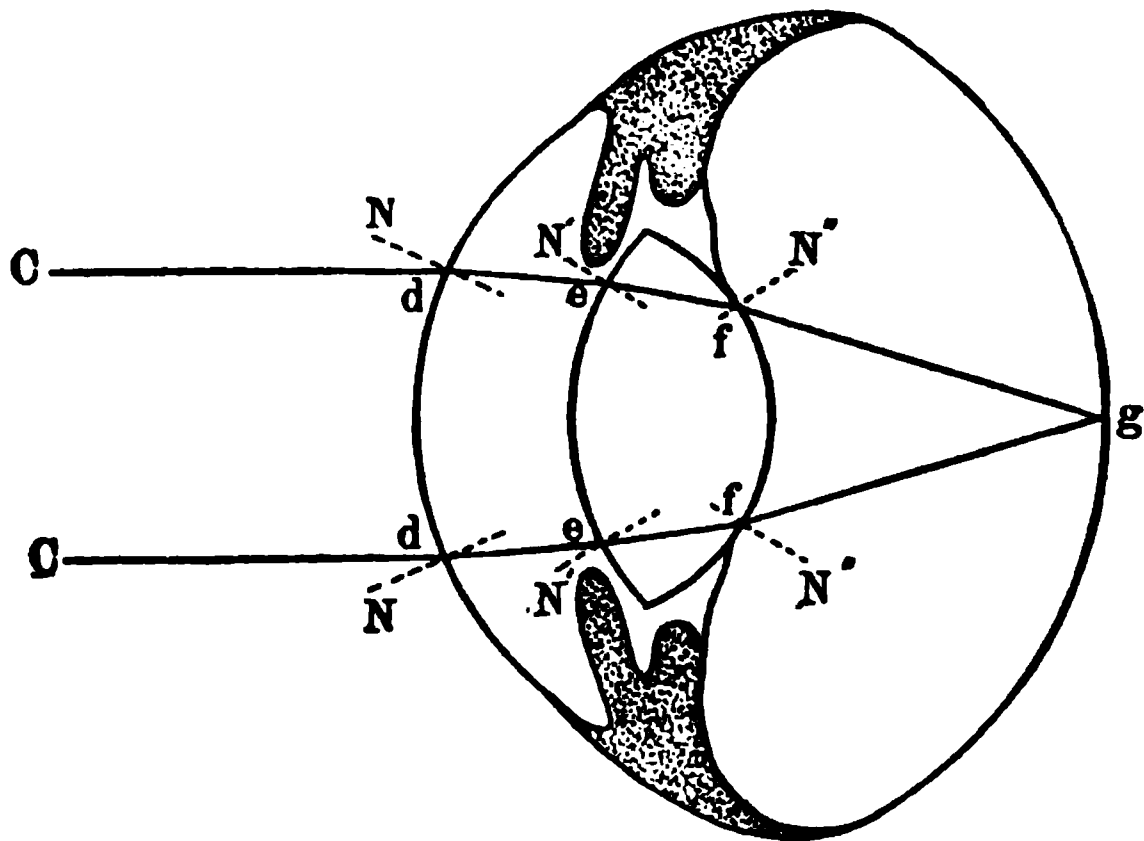
Fig. 149.—Diagram illustrating the surfaces at which light is refracted in the eye.

quite plainly if we choose (unless they be very near indeed), there must exist some means by which the eye is focussed or *accommodated* for looking at objects at different distances. That some change does occur one can, also, readily prove by observing that we cannot see distinctly, at the same moment, both near and distant objects. For example standing behind

a lace curtain, at a window, we can as we choose look at the threads of the lace or at the houses across the street; but when we look at the one we see the other only indistinctly; and if, after looking at the more distant object, we look at the nearer we experience a distinct sense of effort. It is clear, then, that something in the eye is different in the two cases. The resting eye, suited for distinctly seeing distant objects, might conceivably be accommodated for near vision in several ways. The refracting indices of its media might be increased; that of course does not happen; the physical properties of the media are the same in both cases: or the distance of the retina from the refracting surfaces might be increased, for example by compression of the eyeball by the muscles around it; however, experiment shows that changes of accommodation can, by stimulating the third cranial nerve, be brought about in the fresh excised eyes of animals from which the muscles lying outside the eyeball have been removed, in which no such compression is possible; we are thus reduced to the third explanation, that the refracting surfaces, or some of them, become more curved, and so bring diverging rays sooner to a focus; for a lens of smaller curvature is more converging than one of greater curvature composed of the same material. Observation shows that this is what actually happens: the corneal surface remains unchanged when a near object is looked at after a distant one, but the anterior surface of the lens becomes considerably more convex and the posterior slightly so. As already pointed out, when light meets the separating surface of two media some is reflected and some refracted. If, therefore, a person be taken into a dark room and a candle be held on one side of his eye while he looks at a distant object, an observer can see three images of the flame in his pupil, due to that portion of the light reflected from the surfaces between the

Fig. 150.—The images of a candle-flame as seen reflected from the refracting media of the eye.

media. One image (*a*, Fig. 150) is erect and bright, reflected from the convex mirror formed by the cornea; the next, *b*, is dimmer and also erect; it comes from the front of the lens. The third, *c*, is dim and *inverted*, being reflected from the concave mirror (see Physics) formed by the back of the lens. When the curvature of a curved mirror is altered the size of

the image reflected from it is also altered, becoming smaller when the radius of curvature of the mirror is lessened and *vice versa.* If the three images be carefully watched while the observed eye looks at a near object in the same line as the distant point previously looked at, it is seen that the image due to corneal reflection remains unchanged; that due to light from the front of the lens becomes smaller and brighter; the image from the back of the lens also becomes very slightly smaller. The change in the curvature of the front of the lens can be calculated from the change in size of the image reflected from it when the eye changes from distant to near accommodation. When a distant object is looked at the radius of curvature is 10 mm. ($\frac{2}{5}$ inch), when a very near about 6 mm. ($\frac{6}{25}$ inch), and this change is sufficient to account for the range of accommodation of the normal eye.

When the eye is focussed for seeing a near object the circular muscle of the iris contracts, narrowing the pupil, but this has nothing directly to do with the accommodation.

Accommodation is brought about mainly by the ciliary muscle (Fig. 151). In the resting eye it is relaxed and the suspensory ligament of the lens is taut, and, pulling on its edge, drags it out laterally a little and flattens its surfaces,
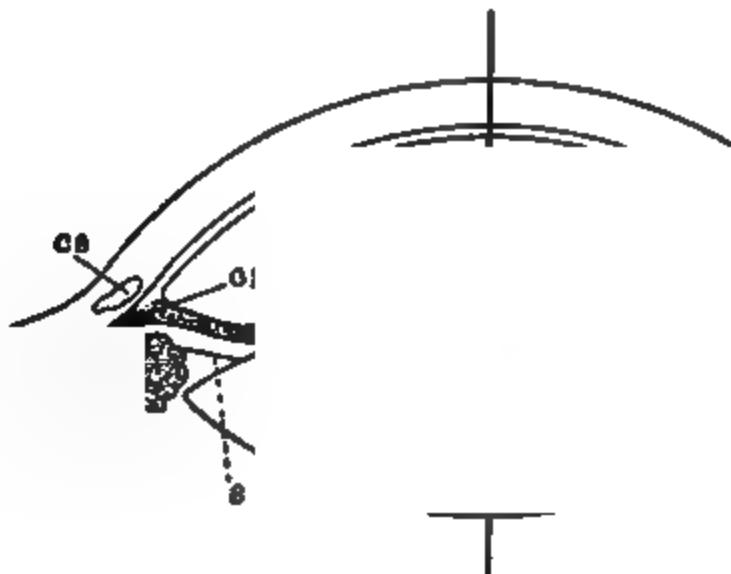
Fig. 151.—Diagram to illustrate the mechanism of accommodation; on the right half of the figure for a near, on the left for a distant, object: *cs,* canal of Schlemm; *cf,* circular portion of ciliary muscle: *rf,* radial portion of ciliary muscle; *ch,* ciliary process of choroid; *sl,* suspensory ligament; *i,* iris.

especially the anterior, since the ligament is attached a little in front of the edge. To see a nearer object the ciliary muscle is contracted, and according to the degree of its contraction slackens the suspensory ligament, and then the elastic lens, relieved from the lateral drag, bulges out a little in the centre,

Short Sight and Long Sight. In the eye the range of accommodation is very great, allowing the rays from points infinitely distant up to those from points about eight inches in front of the eye to be brought to a focus on the retina. In the normal eye parallel rays meet on the retina when the ciliary muscle is completely relaxed (*A*, Fig. 152). Such eyes are *emmetropic*. In other eyes the eyeball is too long from before back; in the resting state parallel rays meet in front of the retina (*B*). Persons with such eyes, therefore, cannot see

Fig. 152.—Diagram illustrating the path of parallel rays after entering an emmetropic (*A*), a myopic (*B*), and a hypermetropic (*C*) eye.

distant objects distinctly without the aid of diverging (concave) spectacles; they are *short-sighted* or *myopic*. Or the eyeball may be too short from before back; then, in the resting state, parallel rays are brought to a focus behind the retina (*C*). To see even infinitely distant objects, such persons must therefore use their accommodating apparatus to increase the converging power of the lens; and when objects are near they cannot, with the greatest effort, bring the divergent rays proceeding from them to a focus soon enough. To get distinct retinal images of near objects they therefore need converging (convex) spectacles. Such eyes are called *hypermetropic*, or in common language *long-sighted*.

Hygienic Remarks. Since muscular effort is needed by the normal eye to see near objects, it is clear why the prolonged contemplation of such is more fatiguing than looking at more distant things. If the eye be hypermetropic still more is this apt to be the case, for then the ciliary muscle has no rest when the eye is used, and to read a book at a distance such that enough light is reflected from it into the eye in order to enable the letters to be seen at all, requires an extraordinary effort of accommodation. Such persons complain that they can read well enough for a time, but soon fail to be able to see distinctly. This kind of weak sight should always lead to examination of the eyes by an oculist, to see if glasses are needed; otherwise severe neuralgic pains about the eyes are apt to come on, and the overstrained organ may be permanently injured. Old persons are apt to have

such eyes; but young children frequently also possess them, and if so should at once be provided with spectacles.

Short-sighted eyes appear to be much more common now than formerly, especially in those given to literary pursuits. Myopia is rare among those who cannot read or who live mainly out of doors. It is not so apt to lead to permanent injury of the eye as is the opposite condition, but the effort to see distinctly objects a little distant is apt to produce headaches and other symptoms of nervous exhaustion. If the myopia become gradually worse the eyes should be rested for several months. Short-sighted persons are apt to have, or acquire, peculiarities of appearance: their eyes are often prominent, indicative of the abnormal length of the eyeball. They also get a habit of "screwing" up the eyelids, probably an indication of an effort to compress the eyeball from before back so that distant objects may be better seen. They often stoop, too, from the necessity of getting their eyes near objects they want to see. The acquirement of such habits may be usually prevented by the use of proper glasses. On the other hand "it is said that myopia even induces peculiarities of character, and that myopes are usually unsuspicious and easily pleased; being unable to observe many little matters in the demeanor or expression of those with whom they converse, which, being noticed by those of quicker sight, might induce feelings of distrust or annoyance."

In old age the lens loses some of its elasticity and becomes more rigid. This leads to the long-sightedness of old people, known as *presbyopia*. The stiffer lens does not become as convex as it did in early life, when the ciliary muscle contracts and the suspensory ligament is relaxed. A special effort of accommodation is therefore needed in order to adapt the eye to see near objects distinctly; and convex glasses are required.

In all forms of deficient accommodation too strong glasses will injure the eyes irreparably, increasing the defects they are intended to relieve. Skilled advice should therefore be invariably obtained in their selection, except perhaps in the long-sightedness of old age, when the sufferer may tolerably safely select for himself any glasses that allow him to read easily a book about 30 centimeters (12 inches) from the eye. As age advances stronger lenses must usually be obtained.

Optical Defects of the Eye. The eye, though it answers

admirably as a physiological instrument, is by no means per-
fect optically; not nearly so good, for example, as a good
microscope objective. The main defects in it are due to—

1. *Chromatic Aberration.* As already pointed out, the
rays at the violet end of the solar spectrum are more refran-
gible than those at the red end. Hence they are brought to a
focus sooner. The light emanating from a point on a white
object does not, therefore, all meet in one point on the retina;
but the violet rays come to a focus first, then the indigo, and
so on to the red, farthest back of all. If the eye is accommo-
dated so as to bring to a focus on the retina parallel red rays,
then violet rays from the same source will meet half a milli-
meter in front of it, and crossing and diverging there make
a little violet *circle of diffusion* around the red point on the
retina. In optical instruments this defect is remedied by
combining together lenses made of different kinds of glass;
such compound lenses are called *achromatic.*

The general result of chromatic aberration, as may be seen
in a bad opera-glass, is to cause colored borders to appear
around the edges of the images of objects. In the eye we
usually do not notice such borders unless we especially look
for them; but if, while a white surface is looked at, the edge
of an opaque body be brought in front of the eye so as to
cover half the pupil, colorations will be seen at its margin.
If accommodation be inexact they appear also when the
boundary between a white and a black surface is observed.
The phenomena due to chromatic aberration are much more
easily seen if light containing only red and violet rays be used
instead of white light containing all the rays of intermediate
refrangibility. Ordinary blue glass only lets through these two
kinds of rays. If a bit of it be placed over a very small hole
in an opaque shutter and sunlight be admitted through the
hole, it will be found that with one accommodation (that for
the red rays) a red point is seen with a violet border, and
with another (that at which violet rays are brought to a focus
on the retina) a violet point is seen with a red aureole.

2. *Spherical Aberration.* It is not quite correct to state
that ordinary lenses bring to a focus in one point behind them
rays proceeding from a point in front, even when these are
all of the same refrangibility. Convex lenses whose surfaces
are segments of spheres, as are those of the eye, bring to a
focus sooner the rays which pass through their marginal than

those passing through their central parts. If rays proceeding from a point and traversing the lateral part of a lens be brought to a focus at any point, then those passing through the centre of the lens will not meet until a little beyond that point. If the retina receive the image formed by the peripheral rays the others will form around this a small luminous circle of light—such as would be formed by sections of the cones of converging rays in Fig. 140, taken a little in front of *r r.* This defect exists in all glass lenses, as it is found impossible in practice to grind them of the non-spherical curvatures necessary to avoid it. In our eyes its effect is to a large extent corrected in the following ways—(*a*) The opaque iris cuts off many of the external and more strongly refracted rays, preventing them from reaching the retina. (*b*) The outer layers of the lens are less refracting than the central; hence the rays passing through its peripheral parts are less refracted than those passing nearer its axis.

3. *Irregularities in Curvature.* The refracting surfaces of our eyes are not even truly spherical; this is especially the case with the cornea, which is very rarely curved to the same extent in its vertical and horizontal diameters. Suppose the vertical meridian to be the most curved; then the rays proceeding from points along a vertical line will be brought to a focus sooner than those from points on a horizontal line. If the eye is accommodated to see distinctly the vertical line, it will see indistinctly the horizontal and *vice versa.* Few people therefore see equally clearly at once two lines crossing one another at right angles. The phenomenon is most obvious, however, when a series of concentric circles (Fig. 153) is looked at: then when the lines appear sharp along some sectors, they are dim along the rest. When this defect, known as *astigmatism,* is marked it causes serious troubles of vision and requires peculiarly shaped glasses to counteract it.

4. *Opaque Bodies in the Refracting Media.* In diseased eyes the lens may be opaque (*cataract*) and need

Fig. 153.

removal; or opacities from ulcers or wounds may exist on the cornea. But even in the best eye there are apt to be small opaque bodies in the vitreous humor causing *muscæ volitantes;* that is, the appearance of minute bodies floating in space outside the eye, but changing their position when the position of the eye changes, by which fact their origin in internal causes may be recognized. Many persons never see them until their attention is called to their sight by some weakness of it, and then they think they are new phenomena. Visual phenomena due to causes in the eye itself are called *entoptic;* the most interesting are those due to the retinal blood-vessels (Chap. XXXIII.). Tears, or bits of the secretion of the Meibomian glands, on the front of the eyeball often cause distant luminous objects to look like ill-defined luminous bands or patches of various shape. The cause of such appearances is readily recognized, since they disappear or are changed after winking.

CHAPTER XXXIII.

THE EYE AS A SENSORY APPARATUS.

The Excitation of the Visual Apparatus.—The excitable visual apparatus for each eye consists of the retina, the optic nerve, and the brain-centres connected with the latter; however stimulated, if intact, it causes visual sensations. In the great majority of cases its excitant is objective light, and so we refer all stimulations of it to that cause, unless we have special reason to know the contrary. As already pointed out pressure on the eyeball causes a luminous sensation (phosphene), which suggests itself to us as dependent on a luminous body situated in space where such an object must be in order to excite the same part of the retina. Since all rays of light penetrating the eye, except in the line of its long axis, cross that axis, if we press the outer side of the eyeball we get a visual sensation referred to a luminous body on the nasal side; if we press below we see the luminous patch above, and so on.

Of course different rays entering the eye take different paths through it, but on general optical principles, which cannot here be detailed, we may trace all oblique rays through the organ by assuming that they meet and leave the optic axis at what are known as the *nodal points* of the system; these (*kk′*, Fig. 154) lie near together in the lens. If we want to find where rays of light from *A* will meet the retina (the eye being properly accommodated for seeing an object at that distance) we draw a line from *A* to *k* (the first nodal point) and then another, parallel to the first, from *k′* (the second nodal point) to the retina. The nodal points of the eye lie so near together that for practical purposes we may treat them as one (*k*, Fig. 155), placed near the back of the lens. By manifold experience we have learnt that a luminous body (*A*, Fig. 155) which we see, always lies on the prolongation of the line joining the excited part of the retina,

a, and the nodal point *k*. Hence any excitation of that part of the retina makes us think of a luminous body somewhere on the line *a A*, and, similarly, any excitation of *b*, of a body
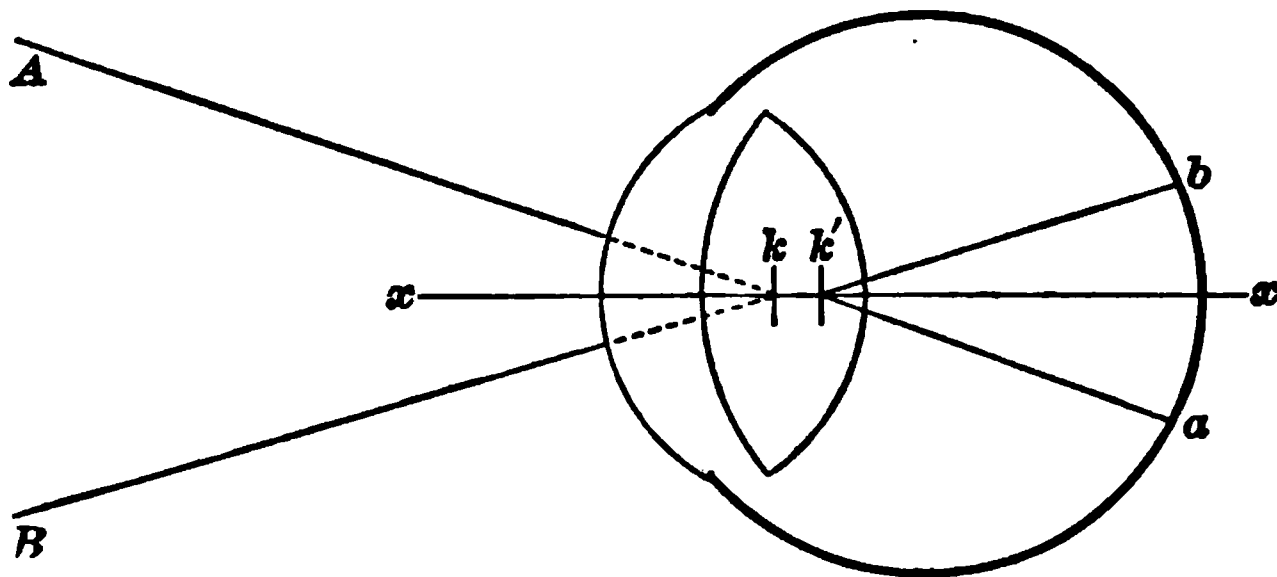
Fig. 154.—Diagram illustrating the points at which incident rays meet the retina. *xx*, optic axis ; *k*, first nodal point; *k'*, second nodal point; *b*, point where the image of *B* would be formed, were the eye properly accommodated for it ; *a*, the retinal point where the image of *A* would be formed.

on the line *b B* or its prolongation. It is only other conflicting experiences, as that with the eyes closed external bodies do not excite visual sensations, and the constant connection
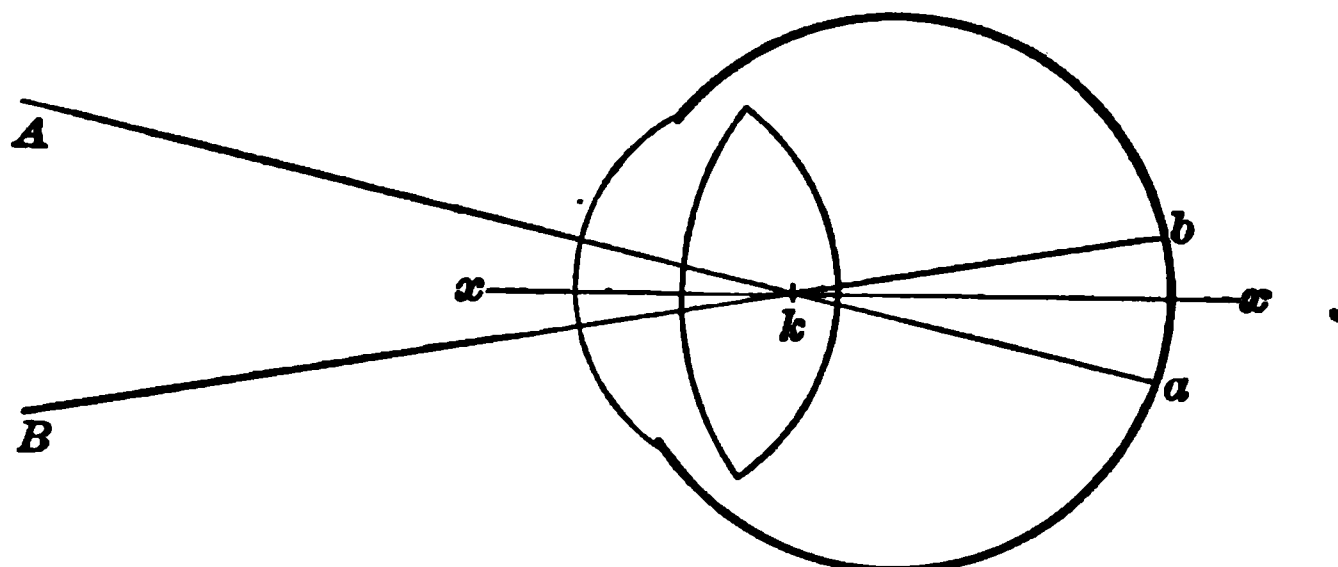
Fig. 155.—Diagrammatic section through the eyeball. *xx*, optic axis ; *k*, nodal point.

of the pressure felt on the eyelid with the visual sensation, that enable us when we press the eyeball to conclude that, in spite of what we seem to *see*, the luminous sensation is not due to objective light from outside the eye.

The Idio-Retinal Light.—The eyelids are not by any means perfectly opaque ; in ordinary daylight they still allow a considerable quantity of light to penetrate the eye, as any one may observe by passing his hand in front of the closed eyes. But even in a dark room with the eyes completely covered up so that no objective light can enter them, there is still experienced a small amount of visual sensation due to

internal causes. The field of vision is not absolutely dark but slightly luminous, with brighter fleeting patches traversing it. These are especially noticeable, for example, in trying to see and grope one's way with the eyes open up a perfectly dark staircase. Then the luminous patches attract special attention because they are apt to be taken for the signs of objective realities; they become very manifest when any sudden jar of the Body, due for example to knocking against something, occurs; and have no doubt given rise to many ghost stories. These visual sensations felt in the absense of all external stimulation of the eyes, may for convenience be spoken of as due to the *idio-retinal light.*

The Excitation of the Visual Apparatus by Light.— Light only excites the retina when it reaches its nerve end organs, *the rods and cones.* The proofs of this are several.

FIG. 156.

1. *Light does not arouse visual sensations when it falls directly on the fibres of the optic nerve.* Where this nerve enters there is a retinal part possessing only nerve-fibres, and this part is blind. Close the left eye and look steadily with the right at the cross in Fig. 156, holding the book vertically in front of the face, and moving it to and fro. It will be found that at about 25 centimeters (10 inches) off the white circle disappears; but when the page is nearer or farther, it is seen. During the experiment the gaze must be kept fixed on the cross. There is thus in the field of vision a *blind spot,* and it is easy to show by measurement that it lies where the optic nerve enters.

When the right eye is fixed on the cross, it is so directed that rays from this fall on the yellow spot (*y*, Fig. 157). The rays from the circle then cross the visual axis at the nodal point, *n*, and meet the retina at *o*. If the distance of the nodal point of the eye from the paper be *f*, and from

the retina (which is 15mm.) be F, then the distance, on the paper, of the cross from the circle will be to the distance of y from o as f is to F. Measurements made in this way show that the circle disappears when its image is thrown on the entry of the optic nerve, which lies to the nasal side of the yellow spot.

2. The above experiment having shown that light does not act directly on the optic nervefibres any more than it does on any other nervefibres, we have next to see in what part of the retina those changes do first occur which form the link between light and nervous impulses. *They occur in the outer part of the retina, in the rods and cones.* This is proved by what is called Purkinje's experiment. Take a candle into a dark room and look at a surface not covered with any special pattern, say a whitewashed wall

Fig. 157.

or a plain window-shade. Hold the candle to the side of one eye and close to it, but so far back that no light enters the pupil from it; that is so far back that the flame just cannot be seen, but so that a strong light is thrown on the white of the eye as far back as possible. Then move the candle a little to and fro. The surface looked at will appear luminous with reddish-yellow light, and on it will be seen dark branching lines which are the shadows of the retinal vessels. Now in order that these shadows may be seen the parts on which the light acts must be behind the vessels, that is in the outer layers of the retina since the blood vessels lie in its inner strata. The experiment may be more satisfactorily performed by getting another person to focus with a lens the light of the candle as a bright spot as far back as possible on the white of the observer's eye.

If the light be kept steady the vascular shadows soon disappear ; in order to continue to see them the candle must be kept moving. The explanation of this fact may readily be made clear by fixing the eyes for ten or fifteen seconds on the dot of an " i " somewhere about the middle of this page : at first the distinction between the slightly luminous black letters and the highly luminous white page is very obvious ; in other words, the different sensations arising from the strongly and the feebly excited areas of the retina. But if

the glance do not be allowed to wander, very soon the letters become indistinct and at last disappear altogether ; the whole page looks uniformly grayish. The reason of this is that the powerful stimulation of the retina by the light reflected from the white part of the page soon fatigues the part of the visual apparatus it acts upon ; and as this fatigue progresses the stimulus produces less and less effect. The parts of the retina, on the other hand, which receive light only from the black letters are but little stimulated and retain much of their original excitability, so that, at last, the feebler excitation acting upon these more irritable parts produces as much sensation as the stronger stimulus acting upon the fatigued parts; and the letters become indistinguishable. To see them continuously we must keep shifting the eyes so that the parts of the visual apparatus are alternately fatigued and rested, and the general irritability of the whole is kept about the same. So, in Purkinje's experiment, if the position of the shadows remain the same, the shaded part of the retina soon becomes more irritable than the more excited unshaded parts, and its relative increase of irritability makes up for the less light falling on it, so that the shadows cease to be perceived. It is for this reason that we do not see the retinal vessels under ordinary circumstances. When light, as usual, enters the eye from front through the pupil the shadows always fall on the same parts of the retina, and these parts are thus kept sufficiently more excitable than the rest to make up for the less light reaching them through the vessels. To see the latter we must throw the light into the eye in an unusual direction, not through the pupil but laterally through the sclerotic. If

FIG 158.

v, Fig. 158, be the section of a retinal vessel, ordinarily its shadow will fall at some point on a line prolonged through it from the centre of the pupil. If a candle flame be held opposite *b* it illuminates that part of the sclerotic and from there light radiates and illumines the interior of the eye. The resulting sensation we refer to light entering the eye in the usual manner through the pupil, and accordingly see the surface we look at as if it were illuminated. The shadow of *v*, is now cast on an unusual spot *c*, and we see it as if at the

point *d* on the wall, on the prolongation of the line joining the nodal point, *k*, of the eye with *c*. If the candle be moved so as to illuminate the point *b'* of the sclerotic, the shadow of *v* will be cast on *c'* and will accordingly seem on the wall to move from *d* to *d'*. It is clear that if we know how far *b* is from *b'*, how far the wall is from the eye, and how far the nodal point is from the retina (15 mm. or 0.6 inch), and measure the distance on the wall from *d* to *d'*, we can calculate how far *c* is from *c'*: and then how far the vessel throwing the shadow must be in front of the retinal parts perceiving it. In this way it is found that the part seeing the shadow, that is the layer on which light acts, is just about as far behind the retinal vessels as the main vascular trunks of the retina are in front of the rod and cone layer. It is, therefore, in that layer that the light initiates those changes which give rise to nervous impulses ; which is further made obvious by the fact that the seat of most acute vision is the *fovea centralis*, where only this layer and the cone-fibres diverging from it are present. When we want to see anything distinctly we always turn our eyes so that its image shall fall on the centres of the yellow spots.

The Vision Purple. How light acts in the retina so as to produce nerve stimuli is still uncertain. Recent observations show that it produces chemical changes in the rod and cone layer, and seemed at first to indicate that its action was to produce substances which were chemical excitants of nerve-fibres ; but although there can be little doubt that these chemical changes play some important part in vision, what their rôle may be is at present quite obscure. If a perfectly fresh retina be excised rapidly, its outer layers will be found of a rich purple color. In daylight this rapidly bleaches, but in the dark persists even when putrefaction has set in. In pure yellow light it also remains unbleached a long time, but in other lights disappears at different rates. If a rabbit's eye be fixed immovably and exposed so that an image of a window is focused on the same part of its retina for some time, and then the eye be rapildy excised in the dark and placed in solution of potash alum, a colorless image of the window is found on the retina, surrounded by the visual purple of the rest which is, through the alum, fixed or rendered incapable of change by light. Photographs, or *optograms*, are thus obtained which differ from the photographer's in that he uses

light to produce chemical changes which give rise to colored bodies, while here the reverse is the case. If the eye be not rapidly excised and put in the alum after its exposure, the optogram will disappear; the vision purple being rapidly regenerated at the bleached part. This reproduction of it is due mainly to the cells of the pigmentary layer of the retina, which in living eyes exposed to light thrust long processes between the rods and cones. Portions of frogs' retinas raised from this, bleach more rapidly than those left in contact with it, but become soon purple again if let fall back upon the pigment-cells. Experiments show, however, that animals (frogs) exposed for a long time to a bright light may have their retinas completely bleached and still see very well; they can still unerringly catch flies that come within their reach; and they can also distinguish colors, or at least some colors, as green. Moreover, the vision purple is only found in the outer segments of the rods; there is none in the cones, and yet these alone exist in the yellow spot of the human eye, which is the seat of most acute vision; and animals, such as snakes, which have only cones in the retina, possess no vision purple and nevertheless see very well.

It may be that other bodies exist in the retina which are also chemically changed by light, but the changes of which are not accompanied by alterations in color which we can see; and, in the absence of the vision purple, seeing might be carried on by means of these, which may be less quickly destroyed by light and so still persist in the bleached retinas of the frogs above mentioned. For the present, however, the question of the part, if any, played in vision by such bodies must be left an open one : and the possibility that the rods and cones form an apparatus which directly converts ethereal vibrations into nerve stimuli without any intervening chemical process must be borne in mind.

The Intensity of Visual Sensations. Light considered as a form of energy may vary in quantity ; physiologically, also, we distinguish quantitative differences in light as degrees of brightness, but the connection between the intensity of the sensation excited and the quantity of energy represented by the stimulating light is not a direct one. In the first place, some rays excite our visual apparatus more powerfully than others : a given amount of energy in the form of yellow light, for example, causes more powerful visual sensations than the

same quantity of energy in the form of violet light; and ultra-violet rays only become visible, and then very faintly, when all others are suppressed; but if they be passed through some fluorescent substance (see Physics), such as an acid solution of quinine sulphate, which, without altering the amount of energy, turns it into ethereal oscillations of a longer period, then the light becomes readibly perceptible.

Even with light-rays of the same oscillation period our sensation is not proportional to the amount of energy in the light; to the amount of heat, for example, to which it would give rise if all transformed into it. If objective light increase gradually in amount our sensation increases also, up to a limit beyond which it does not go, no matter how strong the light becomes; but the increase of sensation takes place far more slowly than that of the light, in accordance with the psycho-physical law already mentioned. If we call the amount of light given out by a single candle a, then that emitted by two candles will be $2a$; and so on. If the amount of sensation excited by the single candle be A, then that due to two candles will not be $2A$, and that by three will be far less than $3A$. If a white surface, P, Fig 159, be illuminated by a candle at c and another elsewhere, and a rod, o, be placed so as to in-tercept the light from c, but not that from the other candle, we see clearly a shadow, since our eyes recognize the difference in luminosity of this part of the paper, reflecting light from one candle only, from that of the rest which is illuminated
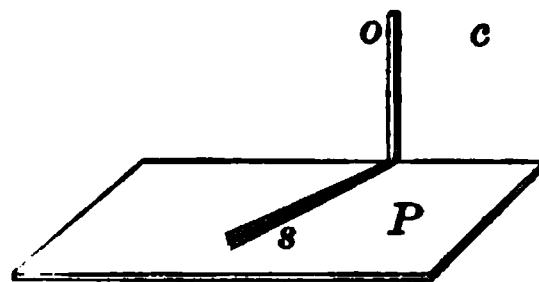
Fig. 159

by two: that is we can tell the sensation due to the stimulus a from that due to the stimulus $2a$.) If now a bright lamp be brought in and placed alongside, and its light be physically equal to that of 10 candles, we cease to perceive the shadow s. We find the sensation aroused by objective light $= 12a$ (due to the lamp and two candles) cannot be told from that due to light $= 11a$; although the difference of objective light is still $1a$ as before. Most persons must have observed illustrations of this. Sitting in a room with three lights not unfrequently some object so intercepts the light from two as to cast on the wall two shadows which partly overlap. Where the shadows overlap the wall gets light only from the third candle; around that, where each shadow is separate, it is illuminated by this

and one other candle; and the wall in the neighborhood of the shadows by all three. Objectively, therefore, the difference between the deep shadow and half shadow is that between the light of one candle and that of two. The difference between the half shadows and the wall around is that between the light of two and three candles. But as a matter of sensation the difference between the half shadow and the full shadow seems much greater than that between the half shadow and the rest of the wall; in other words the difference, a, between a and $2a$, is a more efficient stimulus than the same difference, a, between $2a$ and $3a$. When the total stimulus increases the same absolute difference is less felt or may be entirely unperceived. An example of this which every one will recognize is afforded by the invisibility of the stars in daytime.

On the other hand, as the total stimulus increases or decreases the same fractional difference of the whole is perceived with the same ease; *i.e.*, excites the same amount of sensation. In reading a book by lamplight we perceive clearly the difference between the amount of light reflected from the black letters and the white page. If we call the total lamplight reflected by the blank parts $10a$ and that by the letters $2a$, we may say we perceive with a certain distinctness a luminous difference equal to one fifth of the whole. If we now take the book into the daylight the total light reflected from the letters and the unprinted part of the page increases, but in the same proportion. Say the one now is $50a$ and the other $10a$; although the absolute difference between the two is now $40a$ instead of $8a$ we do not see the letters any more plainly than before. The smallest difference in luminous intensity which we can perceive is about $\frac{1}{100}$ of the whole, for all the range of lights we use in carrying on our ordinary occupations. For strong lights the smallest perceptible fraction is considerably greater; finally we reach a limit where no increase in brightness is felt. For weak illumination the sensation is more nearly proportioned to the total differences of the objective light. Thus in a dark room an object reflecting all the little light that reaches it appears almost twice as bright as one reflecting only half; in a stronger light it would so appear. Bright objects in general obscurity thus appear unnaturally bright when compared with things about them, and indeed often look self-luminous.

A cat's eyes, for example, are said to "shine in the dark"; and painters to produce moonlight effects always make the bright parts of a picture relatively brighter, when compared with things about them, than would be the case if a sunny scene were to be represented; by a relatively excessive use of white pigment they produce the relatively great brightness of those things which are seen at all in the general obscurity of a moonlight landscape.

The Duration of Luminous Sensations.—This is greater than that of the stimulus, a fact taken advantage of in making fireworks: an ascending rocket produces the sensation of a trail of light extending far behind the position of the bright part of the rocket itself at the moment, because the sensation aroused by it in a lower part of its course still persists. So, shooting stars appear to have luminous tails behind them. By rotating rapidly before the eye a disk with alternate white and black sectors we get for each point of the retina on which a part of its image falls, alternating stimulation (due to the passage of white sector) and rest (when a black sector is passing). If the rotation be rapid enough the sensation aroused is that of a uniform gray, such as would be produced if the white and black were mixed and spread evenly over the disk. In each revolution the eye gets as much light as if that were the case, and is unable to distinguish that this light is made up of separate portions reaching it at intervals: the stimulation due to each lasts until the next begins and so all are fused together. If, while looking at the flame, one turns out suddenly the gas in a room containing no other light, the image of the flame persists a short time after the flame itself is extinguished.

The Localizing Power of the Retina.—As already pointed out a necessary condition of seeing definite objects, as distinguished from the power of recognizing differences of light and darkness, is that all light entering the eye from one point of an object shall be focused on one point of the retina. This, however, would not be of any use had we not the faculty of distinguishing the stimulation of one part of the retina from that of another part. This power the visual apparatus possesses in a very high degree; while with the skin we cannot distinguish from one, two points touching it less than 1 mm. ($\frac{1}{25}$ inch) apart, with our eyes we can distinguish two points whose retinal images are not more than .004 mm.

(.00016 inch) apart. The distance between the retinal images of two points is determined by the "visual angle" under which they are seen; this angle is that included between lines drawn from them to the nodal point of the eye. If *a* and *b* (Fig. 160) are luminous points, the image of *a* will be
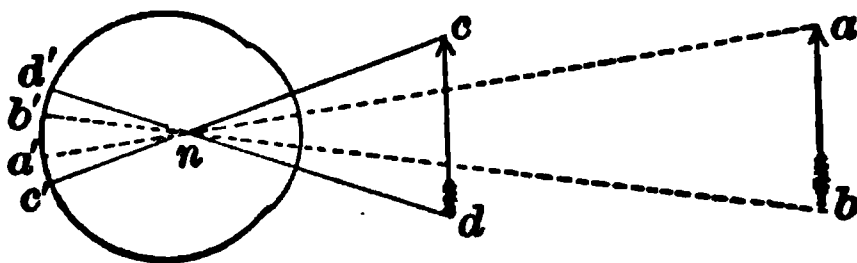
Fig. 160.

formed at *a'* on the prolongation of the line *a n* joining *a* with the node, *n*. Similarly the image of *b* will be formed at *b'*. If *a* and *b* still remaining the same distance apart, be moved nearer the eye to *c* and *d*, then the visual angle under which they are seen will be greater and their retinal images will be farther apart, at *c'* and *d'*. If *a* and *b* are the highest and lowest parts of an object, the distance between their retinal images will then depend, clearly, not only on the size of the object, but on its distance from the eye; to know the discriminating power of the retina we must therefore measure the visual angle in each case. In the fovea centralis two objects seen under a visual angle of 50 to 70 seconds can be distinguished from one another; this gives for the distance between the retinal images that above mentioned, and corresponds pretty accurately to the diameter of a cone in that part of the retina. We may conclude, therefore, that when two images fall on the same cone or on two contiguous cones they are not discriminated; but that if one or more unstimulated cones intervene between the stimulated, the points may be perceived as distinct. The diameter of a rod or cone, in fact, marks the anatomical limit up to which we can by practice raise our acuteness of visual discrimination; and in the yellow spot which we constantly use all our lives in looking at things which we want to see distinctly, we have educated the visual apparatus up to about its highest power. Elsewhere on the retina our discriminating power is much less and diminishes as the distance from the yellow spot increases. This is partly due, no doubt, to a less sensibility of those retinal regions, such as, by other facts, is proved to exist, but in part, no doubt is also due to a want of practice. The more

peripheral the retinal region the less we have used it for such purposes. It is probable, therefore, that outlying portions of the retina are capable of education to a higher discriminating power, just as we shall find the skin to be for tactile stimuli.

While we can tell the stimulation of an upper part of the retina from a lower, or a right region from a left, it must be borne in mind that we have no direct knowledge of which is upper or lower or right or left in the ocular image. All our visual sensations tell us is that they are aroused at different points, and nothing at all about the actual positions of these on the retina. There is no other eye behind the retina looking at it to see the inversion of the image formed on it. Suppose I am looking at a pane in a second-story window of a distant house: its image will then fall on the fovea centralis ; the line joining this with the pane is called the *visual axis*. The image of the roof will be formed on a part of the retina below the fovea, and that of the front door above it. I distinguish that the images of all these fall on different parts of the retina in certain relative positions, and have learnt, by the experience of all my life, that when the image of anything arouses the sensation due to excitation of part of the retina below the fovea the object is above my visual axis, and *vice versa* ; similarly with right and left. Consequently I interpret the stimulation of lower retinal regions as meaning high objects, and of right retinal regions as meaning left objects, and never get confused by the inverted retinal image about which directly I know nothing. A new-born child, even supposing it could use its muscles perfectly, could not, except by mere chance, reach towards an object which it saw; it would grasp at random, not yet having learnt that to reach an object exciting a part of the retina above the fovea needed movement of the hand towards a position in space below the visual axis ; but very soon it learns that things near its brow, that is *up*, excite certain visual sensations, and objects below its eyes others, and similarly with regard to right and left; in time it learns to interpret retinal stimuli so as to localize accurately the direction, with reference to its eyes, of outer objects, and never thenceforth gets puzzled by retinal inversion.

Color Vision.—Sunlight reflected from snow gives us a sensation which we call *white*. The same light sent through a prism and reflected from a white surface excites in us no

white sensation but a number of color sensations, gradating insensibly from red to violet, through orange, yellow, green, blue-green, blue, and indigo. The prism separates from one another light-rays of different periods of oscillation and each ray excites in us a colored visual sensation, while all mixed together, as in sunlight, they arouse the entirely different sensation of white. If the light fall on a piece of black velvet we get still another sensation, that of black; in this case the light-rays are so absorbed that but few are reflected to the eye and the visual apparatus is left at rest. Physically black represents nothing: it is a mere zero—the absence of ethereal vibrations; but, in consciousness, it is as definite a sensation as white, red, or any other color. We do not feel blackness or darkness except over the region of the possible visual field of our eyes. In a perfectly dark room we only feel the darkness in front of our eyes, and in the light there is no such sensation associated with the back of our heads or the palms of our hands, though through these we get no visual sensations. It is obvious, therefore, that the sensation of blackness is not due to the mere absence of luminous stimuli, but to the unexcited state of the retinas, which are alone capable of being excited by such stimuli when present. This fact is a very remarkable one, and is not paralleled in any other sense. Physically, complete stillness is to the ear what darkness is to the eye; but silence impresses itself on us as the absence of sensation, while darkness causes a definite feeling of " blackness."

Young's Theory of Color Vision.—Our color sensations insensibly fade into one another; starting with black we can insensibly pass through lighter and lighter shades of gray to white: or beginning with green through darker and darker shades of it to black or through lighter and lighter to white: or beginning with red we can by imperceptible steps pass to orange, from that to yellow and so on to the end of the solar spectrum: and from the violet, through purple and carmine, we may get back again to red. Black and white appear to be fundamental color sensations mixed up with all the rest: we never imagine a color but as light or dark, that is as more or less near white or black; and it is found that as the light thrown on any given colored surface weakens, the shade becomes deeper until it passes into black; and if the illumination be increased, the color becomes " lighter " until it passes

into white. Of all the colors of the spectrum yellow most
easily passes into white with strong illumination. Black and
white, with the grays which are mixtures of the two, thus
seem to stand apart from all the rest as the fundamental
visual sensations, and the others alone are in common par-
lance named "colors." It has even been suggested that the
power of differentiating them in sensation has only lately
been acquired by man, and a certain amount of evidence has
been adduced from passages in the Iliad to prove that the
Greeks in Homer's time confused together colors that are
very different to most modern eyes; at any rate there seems
to be no doubt that the color sense can be greatly improved
by practice; women whose mode of dress causes them to pay
more attention to the matter, have, as a general rule, a more
acute color sense than men.

Leaving aside black, white, gray, and the various browns
(which are only dark tints of other colors), we may enumer-
ate our color sensations as red, orange, yellow, green, blue,
violet, or purple; between each there are, however, numerous
transition shades, as yellow-green, blue-green, etc., so that
the number which shall have definite names given to them is
to a large extent arbitrary. Of the above, all but purple are
found in the spectrum given when sunlight is separated by a
prism into its rays of different refrangibility; rays of a cer-
tain wave-length or period of oscillation cause in us the feel-
ing red; others yellow, and so on; for convenience we may
speak of these as red, yellow, blue, etc., rays; all together, in
about equal proportions, they arouse the sensation of white.
A remarkable fact is that most color feelings can be aroused
in several ways. White, for example, not only by the above
general mixture, but red and blue-green rays, or orange and
blue, or yellow and violet, taken in pairs in certain propor-
tions, and acting simultaneously or in very rapid succession
on the same part of the retina, cause the sensation of white:
such colors are called *complementary* to one another. The
mixture may be made in several ways; as, for example, by
causing the red and blue-green parts of the spectrum to
overlap, or by painting red and blue-green sectors on a disk
and rotating it rapidly; they cannot be made, however, by
mixing pigments, since what happens in such cases is a very
complex phenomenon. Painters, for example, are accustomed
to produce green by mixing blue and yellow paints, and some

may be inclined to ridicule the statement that yellow and blue when mixed give white. When, however, we mix the pigments we do not combine the sensations of the same name, which is the matter in question. Blue paint is blue because it absorbs all the rays of the sunlight except the blue and some of the green; yellow is yellow because it absorbs all but the yellow and some of the green, and when blue and yellow are mixed the blue absorbs all the distinctive part of the yellow and the yellow does the same for the blue; and so only the green is left over to reflect light to the eye, and the mixture has that color. Grass-green has no complementary color in in the solar spectrum; but with purple, which is made by mixing red and blue, it gives white. Several other colors taken three together, give also the sensation of white. If then we call the light-rays which arouse in us the sensation red, *a*, those giving us the sensation orange *b*, yellow *c*, and so on, we find that we get the sensation white with *a*, *b*, *c*, *d*, *e*, *f*, and *g* all together; or with *b* and *e*, or with *c* and *f*, or with *a*, *d*, and *e* ; our sensation *white* has no determinate relation to ethereal oscillations of a given period, and the same is true for several other colors; yellow feeling, for example, may be excited by ethereal vibrations of one given wavelength (spectral yellow), or by a light containing only such waves as taken separately cause the sensations red and grass-green; in other words a physical light in which there are no waves of the " yellow " length may cause in us the sensation yellow, which is only one more instance of the general fact that our sensations, as such, give us no direct information as to the nature of external forces; they are but signs which we have to interpret. The doctrine of specific nerve energies makes it highly improbable that our different color sensations can all be due to different modes of excitation of exactly the same nerve-fibres; a fibre which when excited alone gives us the sensation red will always give us that feeling when so excited. The simplest method of explaining our color sensations would therefore be to assume that for each there exists in the retina a set of nerve-fibres with appropriate terminal organs, each excitable by its own proper stimulus. But we can distinguish so innumerable and so finely graded colors, that, on such a supposition, there must be an almost infinite number of different end organs in the retina, and it is more reasonable to suppose that there are a limited

number of primary color sensations, and that the rest are due to combinations of these. That a compound color sensation may be very different from its components when these are regarded apart, is clearly shown by the sensation white aroused either by what we may call red and blue-green, or green and purple, stimuli acting together; or of yellow due to grass-green and red. To account for our various color sensations we may, therefore, assume a much smaller number of primary sensations than the total number of color sensations we experience; all can in fact be explained by assuming any three primary color sensations which together give white, and regarding all the rest as due to mixtures of these in various proportions; there may be more than three, but three will account for all the phenomena, black being a sensation experienced when all visual stimuli are absent. This is known as *Young's theory of color vision,* and is that at present most commonly accepted. The selection of the three primary sensations is decided by the phenomena of color-blindness, which show that if this theory of color vision be correct red must be one of the primary color sensations: if so, then green and violet must be the other two. The theory further assumes that all kinds of light stimulating the end apparatuses give rise to all three sensations, but not necessarily in the same proportion. When all are equally aroused the sensation is white or some shade of gray when the red and green are tolerably powerfully excited and the violet little, the sensation is yellow; when the green powerfully and the red and violet little, the sensation is green, and so on. In this way we can also explain the fact that all colored surfaces when intensely illuminated pass into white. A red light, for example, excites the primary red sensation most, but green and violet a little; as the light becomes stronger a limit is reached beyond which the red sensation cannot go, but the green and violet go on increasing with the intensity of the light, until they too reach their limits; and all three primary sensations being then equally aroused, the sensation white is produced.

Color Blindness. Some persons fail to distinguish colors which are to others quite different; when such a deficiency is well marked it is known as " color blindness," and, assuming Young's theory to be correct, it may be explained by an absence of one or more of the three primary color sensations;

observation of color-blind persons thus helps in deciding which these are. The most common form is red color blindness; persons afflicted with it confuse reds and greens. Red to the normal eye is red because it excites red sensation much, green some, and violet less; and a white page white, because it excites red, green, and violet sensations about equally. In a person without red sensation a red object would arouse only some green and violet sensation and so would be indistinguishable from a bluish green; in practice it is found that many persons confound these colors. Cases of green and violet color blindness are also met with, but they are much rarer than the red color blindness or "Daltonism."

The detection of color blindness is often a matter of considerable importance, especially in sailors and railroad officials, since the two colors most commonly confounded, red and green, are those used in maritime and railroad signals. Persons attach such different names to colors that a decision as to color blindness cannot be safely arrived at by simply showing a color and asking its name. The best plan is to take a heap of worsted of all tints, select one, say a red, and tell the man to put alongside it all those of the same color, whether of a lighter or a darker shade; if red blind he will select not only the reds but the greens, especially the paler tints. About one man in eight is more or less red blind. The defect is much rarer in women.

Fatigue of the Retina. The nervous visual apparatus is easily fatigued. Usually we do not observe this because its restoration is also rapid, and in ordinary life our eyes, when open, are never at rest; we move them to and fro, so that parts of the retina receive light alternately from brighter and darker objects and are alternately excited and rested. How constant and habitual the movement of the eyes is can be readily observed by trying to fix for a short time a small spot without deviating the glance; to do so for even a few seconds is impossible without practice. If any small object is steadily "fixed" for twenty or thirty seconds it will be found that the whole field of vision becomes grayish and obscure, because the parts of the retina receiving most light get fatigued, and arouse no more sensation than those less fatigued and stimulated by light from less illuminated objects. Or look steadily at a black object, say a blot on a white page, for twenty seconds, and then turn the eye on a white wall; the latter

will seem dark gray, with a white patch on it; an effect due to the greater excitability of the retinal parts previously rested by the black, when compared with the sensation aroused elsewhere by light from the white wall acting on the previously stimulated parts of the visual surface. All persons will recall many instances of such phenomena, which are especially noticeable soon after rising in the morning. Similar things may be noticed with colors; after looking at a red patch the eye turned on a white wall sees a blue-green patch; the elements causing red sensations having been fatigued, the white, mixed light from the wall now excites on that region of the retina only the other primary color sensations. The blending of colors so as to secure their greatest effect depends on this fact; red and green go well together because each rests the parts of the visual apparatus most excited by the other, and so each appears bright and vivid as the eye wanders to and fro; while red and orange together, each exciting and exhausting mainly the same visual elements, render dull, or in popular phrase " kill," one another.

Contrasts. If a well-defined black surface be looked at on a larger white one the parts of the latter close to the black look whiter than the rest, and the parts of the black near the white blacker than the rest; so, also, if a green patch be looked at on a red surface each color is heightened near where they meet. This phenomenon is largely due to fatigue and deficient fixation: the retinal parts not excited and fatigued by the black or the green are brought by a movement of the organ so as to receive light from the white or red surface; phenomena due to this cause are known as those of *successive contrast*. Even in the case of perfect fixation, however, something of the same kind is seen; black looks blacker near white and green greener near red when the eye has not moved in the least from one to the other. A small piece of light gray paper put on a sheet of red, which latter is then covered accurately with a sheet of semi-transparent tissue-paper, assumes the complementary color of the red, *i.e.*, looks bluish green; and gray on a green sheet under similar circumstances looks pink. Such phenomena are known as those of *simultaneous contrast*, and are explained on psychological grounds by those who accept Young's theory of color vision. Just as a medium-sized man looks short beside a tall one, so, it is said, a black surface looks blacker near a white one, or a

gray (slightly luminous white) surface, which feebly excites red, green, and violet sensations, looks deficient in red (and so bluish green) near a deeper red surface. There are, however, certain phenomena of simultaneous contrast which cannot be satisfactorily so explained, and these have led to other theories of color vision, the most important of which is that described in the next paragraph.

Hering's Theory of Vision. Contrasts can be seen with the eyes closed and covered. If we look a short time at a bright object and then rapidly exclude light from the eye, we see for a moment a *positive after-image* of the object, *e.g.*, a window with its frame and panes after a glance at it and then closing the eyes. In these positive after-images the bright and dark parts of the object which was looked at retain their original relationship; they depend on the persistence of retinal excitement after the cessation of the stimulus and usually soon disappear. If an object be looked at steadily for some time, say twenty seconds, and the eyes be then closed, a *negative after-image* is seen. In this the lights and shades of the object looked at are reversed. Frequently a positive after-image becomes negative before disappearing. The negative images are explained commonly by fatigue; when the eye is closed some light still enters through the lids and excites less those parts of the retina previously exhausted by prolonged looking at the brighter parts of the field of vision; or, when all light is rigorously excluded, the self stimulation of the visual apparatus itself, causing the *idio-retinal light*, affects less the exhausted portions, and so a negative image is produced. If we fix steadily for thirty seconds a point between two white squares about 4 mm. ($\frac{1}{6}$ inch) apart on a large black sheet, and then close and cover our eyes, we get a negative after-image in which are seen two dark squares on a brighter surface; this surface is brighter close around the negative after-image of each square, and brightest of all between them. This luminous boundary is called the *corona*, and is explained usually as an effect of simultaneous contrast; the dark after-image of the square it is said makes us mentally err in judgment and think the clear surface close to it brighter than elsewhere; and it is brightest between the two dark squares, just as a middle-sized man between two tall ones looks shorter than if alongside one only. If, however, the after-image be watched it will often

be noticed not only that the light band between the squares is intensely white, much more so than the normal idio-retinal light, but, as the image fades away, often the two dark after-images of the squares disappear entirely with all of the corona, except that part between them which is still seen as a bright band on a uniform grayish field. Here there is no contrast to produce the error of judgment, and from this and other experiments Hering concludes that light acting on one part of the retina produces inverse changes in all the rest, and that this has an important part in producing the phenomena of contrasts. Similar phenomena may be observed with colored objects; in their negative after-images each tint is represented by its complementary, as black is by white in colorless vision.

Endeavoring to exclude such loose general explanations as "errors of judgment," Hering proposes a theory of vision which can only be briefly stated here. We may put all our colorless sensations in a continuous series, passing through grays from the deepest black to the brightest white; somewhere half-way between will be a *neutral gray* which is as black as it is white. We may do something similar with our color sensations; as in gray we see black and white so in purple we see red and blue, and all colors containing red and blue may be put in a series of which one end is pure red, the other pure blue. So with red and yellow, blue and green, yellow and green. If we call to mind the whole solar spectrum from yellow to blue, through the yellow-greens, green, and blue-greens, we get a series in which all but the terminals have this in common that they contain some green. Green itself forms, however, a special point; it differs from all tints on one side of it in containing no yellow, and from all on the other in containing no blue. In ordinary language this is recognized: we give it a definite name of its own and call it *green.* Its simplicity compared with the doubleness of its immediate neighbors entitles it to a distinct place in the color-sensation series. There are three other color sensations which like green are simple and must have specific names of their own; they are red, blue, and yellow. Green may be pure green or yellow-green or blue-green, but never yellow and bluish at once, or reddish. Red may be pure or yellowish or bluish, but never greenish. Red and green are thus mutually exclusive; yellow and blue stand in a similar

relationship. All other color sensations, as orange, suggest two of the above, and may be described as mixtures of them; but they themselves stand out as fundamental color sensations. Moreover, it follows from the above, that more than two simple color sensations are never combined in a compound color sensation.

Since red always excludes green, and yellow blue, we may call them anti-colors (the complementary colors of Young's theory), and are led to suspect that in the visual organ there must occur, in the production of each, processes which prevent the simultaneous production of the other, since there is no *a priori* reason in the nature of things why we should not see red and green simultaneously, as well as red and yellow. Along with our color sensations there is always some colorless from the black-white series; which we recognize in speaking of lighter and darker shades of the same color.

Hering assumes, then, in the retina or some part of the nervous visual apparatus, three substances answering to the black-white, red-green, and yellow-blue sensational series, the construction of each substance being attended with one sensation of its pair, and its destruction with the other. Thus, when construction of the black-white substance exceeds destruction, we get a blackish-gray sensation; when the processes are equal the neutral gray; when destruction exceeds construction a light-gray, and so on. In the other color series similar things would occur; when construction of red-green substance exceeded destruction in any point of the retina we would get, say, a red feeling; if so, then excess of destruction would give green sensation. The intensity of any given simple sensation would depend on the ratio of the difference between the construction and destruction of the corresponding substance, to the sum of all the constructions and destructions of visual substances going on in that part of the visual apparatus : in this way anabolic and katabolic nutritive processes would be the material basis of visual sensations. The intensity of a mixed color sensation would be the sum of the intensities of its factors, and its tint and shade dependent on the relative proportion of these factors. When the construction and destruction of the red-green substance are equal no color sensation is aroused by it; and we get gray, due to those simultaneously occurring changes in the black-white substance which are always present, but were

previously more or less cloaked by the results of the changes in the red-green substance. Red and green in certain proportions cause then a white or gray sensation, not because they supplement one another, as on Young's theory, but because they mutually cancel; and so for other complementary colors.

Moreover, according to Hering, destruction of a visual substance going on in one region of the retina promotes construction and accumulation of that substance elsewhere, but especially in the neighborhood of the excited spot. Hence, when a white square on a black ground is looked at, destruction of the black-white substance overbalances construction in the place, on which the image of the square falls, but around this construction occurs in a high degree. When the eyes are shut, this latter retinal region, with its great accumulation of decomposable material, is highly irritable and, under the internal stimuli causing the idio-retinal light, breaks down comparatively fast, causing the corona, which may be intensely luminous; for with the closed eye the total constructive and destructive processes in the visual apparatus are small, and so the excess of destruction in the coronal region bears a large ratio to the sum of the whole processes. The student must apply this theory for himself to the other phenomena of contrasts and negative images, as also to the gradual disappearance of differences between light and dark objects when looked at for a time with steady fixation; the general key being the principle that anything leading to the accumulation of a visual substance increases its decompositions under given stimulation, and *vice versa.* The main value of Hering's theory is that it attempts to account physiologically for phenomena previously indefinitely explained psychologically by such terms as "errors of judgment," which really leave the whole matter where it was, since if (as we must believe) mind is a function of brain, the errors of judgment have still to be accounted for on physiological grounds, as due to conditions of the nervous system.

The three visual substances, the anabolisms and katabolisms of which according to Hering give rise to color sensations, need not necessarily be in the retina itself: they may be in the central nerve portions of the visual apparatus, being excited through different nerve fibres excited by different lights falling on the retina.

There are difficulties in the way of the full acceptance of either the Young (often called the Young-Helmholtz) theory or the theory of Hering, and the whole doctrine of color vision is still in a very unsettled state.

Visual Perceptions. The sensations which light excites in us we interpret as indications of the existence, form, and position of external objects. The conceptions which we arrive at in this way are known as *visual perceptions.* The full treatment of perceptions belongs to the domain of Psychology, but Physiology is concerned with the conditions under which they are produced.

The Visual Perception of Distance. With one eye our perception of distance is very imperfect, as illustrated by the common trick of holding a ring suspended by a string in front of a person's face, and telling him to shut one eye and pass a rod from one side through the ring. If a pen-holder be held erect before one eye, while the other is closed, and an attempt be made to touch it with a finger moved across towards it, an error will nearly always be made. (If the finger be moved straight on towards the pen it will be touched because with one eye we can estimate direction accurately and have only to go on moving the finger in the proper direction till it meets the object.) In such cases we get the only clue from the amount of effort needed to "accommodate" the eye to see the object distinctly. When we use both eyes our perception of distance is much better; when we look at an object with two eyes the visual axes are converged on it, and the nearer the object the greater the convergence. We have a pretty accurate knowledge of the degree of muscular effort required to converge the eyes on all tolerably near points. When objects are farther off, their apparent size, and the modifications of their retinal images brought about by aërial perspective, come in to help. The relative distance of objects is easiest determined by moving the eyes; all stationary objects then appear displaced in the opposite direction (as for example when we look out of the window of a railway car) and those nearest most rapidly; from the different apparent rates of movement we can tell which are farther and nearer. We so inseparably and unconsciously bind up perceptions of distance with the sensations aroused by objects looked at, that we seem to see distance; it seems at first thought as definite a sensation as color.

That it is not is shown by cases of persons born blind, who have had sight restored later in life by surgical operations. Such persons have at first no visual perceptions of distance: all objects seem spread out on a flat surface in contact with the eyes, and they only learn gradually to interpret their sensations so as to form judgments about distances, as the rest of us did unconsciously in childhood before we thought about such things.

The Visual Perception of Size. The dimensions of the retinal image determine primarily the sensations on which conclusions as to size are based; and the larger the visual angle the larger the retinal image: since the visual angle depends on the distance of an object the correct perception of size depends largely upon a correct perception of distance; having formed a judgment, conscious or unconscious, as to that, we conclude as to size from the extent of the retinal region affected. Most people have been surprised now and then to find that what appeared a large bird in the clouds was only a small insect close to the eye; the large apparent size being due to the previous incorrect judgment as to the distance of the object. The presence of an object of tolerably well-known height, as a man, also assists in forming conceptions (by comparison) as to size; artists for this purpose frequently introduce human figures to assist in giving an idea of the size of other objects represented.

The Visual Perception of a Third Dimension of Space. This is very imperfect with one eye; still we can thus arrive at conclusions from the distribution of light and shade on an object, and from that amount of knowledge as to the relative distance of different points which is attainable monocularly; the different visual angles under which objects are seen also assist us in concluding that objects are farther and nearer, and so are not spread out on a plane before the eye, but occupy depth also. Painters depend mainly on devices of these kinds for representing solid bodies, and objects spread over the visual field in the third dimension of space.

Single Vision with Two Eyes. When we look at a flat object with both eyes we get a similar retinal image in each. Under ordinary circumstances we see, however, not two objects but one. In the habitual use of the eyes we move them so that the images of the object looked at fall on the two yellow spots. A point to the left of this object forms its

image on the inner (right) side of the left eye and the outer (right) side of the right. An object vertically above that looked at would form an image straight below the yellow spot of each eye; an object to the left and above, its image to the inner side and below in the left eye and to the outer side and below in the right eye; and so on. We have learned that similar simultaneous excitations of these *corresponding points* mean single objects, and so interpret our sensations. This at least is the theory of the experiential or *empirical* school of psychologists, though others believe we have a sort of intuition on the subject. When the eyes do not work together, as in the muscular incoördination of one stage of intoxication, then they are not turned so that images of the same objects fall on corresponding retinal points, and the person sees double. When a squint comes on, as from paralysis of the external rectus of one eye, the sufferer at first sees double for the same reason, but after a time he makes new associations of corresponding retinal points, and this is in favor of the empirical theory.

When a given object is looked at, lines drawn from it through the nodal points reach the fovea centralis in each eye. Lines so drawn at the same time from a more distant object diverge less and meet each retina on the inner side of its fovea; but as above pointed out the corresponding points for each retinal region on the inside of the left eye, are on the outside of the right, and *vice versa.* Hence the more distant object is seen double. So, also, is a nearer object, because the more diverging lines drawn from it through the nodal points lie outside of the fovea in each eye. Most people go through life unobservant of this fact; we only pay attention to what we are looking at, and nearly always this makes its images on the two foveæ. That the fact is as above stated may, however, be readily observed. Hold one finger a short way from the face and the other a little farther off; looking at one, observe the other without moving the eyes; it will be seen double. For every given position of the eyes there is a surface in space, all objects on which produce images on corresponding points of the two retinas: this surface is called the *horopter* for that position of the eyes: all objects in it are seen single; all others in the visual field, double.

The Perception of Solidity. When a solid object is

looked at the two retinal images are different. If a truncated pyramid be held in front of one eye its image will be that represented at *P*, Fig. 161. If, however, it be held midway
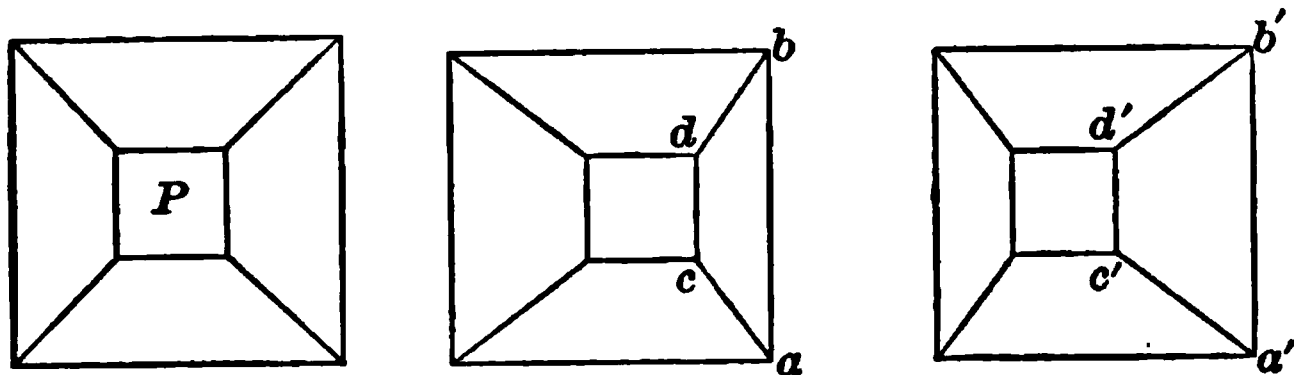
Fig. 161.

between the eyes, and looked at with both, then the left-eye image will be that in the middle of the figure, and the right-eye image that to the right. The small surface, *b d c a*, in one answers to the large surface, *b' d' c' a'*, in the other. This may be readily observed by holding a small cube in front of the nose and alternately looking at it with each eye. In such cases, then, the retinal images do not correspond, and yet we combine them in consciousness so as to see one *solid* object. This is known as *stereoscopic vision*, and the illusion of the common stereoscope depends on it. Two photographs are taken of the same object from two different points of view, one as it appears when seen from the left, and the other when seen from the right. These are then mounted for the stereoscope so that each is looked at by its proper eye, and the object appears in distinct relief, as if, instead of flat pictures, solid objects, occupying three dimensions of space, were looked at. Of course in many stereoscopic views the distribution of light and shade, etc., assist, but these are quite unessential, as may be readily observed by copying the drawings of Fig. 161 and mounting them on a card the size of a stereoscopic slide, and placing it in the instrument. A solid pyramid standing out into space will be distinctly perceived; if the pictures be reversed the pyramid appears hollow. The pictures must not be too different, or their combination to give the idea of a single solid body will not take place. Many persons, indeed, fail entirely to get the illusion with ordinary stereoscopic slides. The phenomena of stereoscopic vision militate strongly against the view that there are any anatomically prearranged corresponding points in the two retinas.

The Perception of Shine. When we look at a rippled

lake in the moonlight, we get the perception of a "shiny" or brilliant surface. The moonlight is reflected from the waves to the eyes in a number of bright points: these are not exactly the same for both eyes, since the lines of light-reflection from the surface of the. water to each are different. The perception of brilliancy seems largely to depend on this slight non-agreement of the light and dark points on the two retinas. A rapid change of luminous points, to and fro between neighboring points on one retina, seems also to produce it.

CHAPTER XXXIV.

THE EAR AND HEARING.

The External Ear. The auditory organ in man consists of three portions, known respectively as the *external ear*, the *middle ear* or *tympanum*, and the *internal ear* or *labyrinth;* the latter contains the end organs of the auditory nerve. The external ear consists of the expansion seen on the exterior of the head, called the *concha, M,* Fig. 162, and a passage leading in from it, the *external auditory meatus, G.*

Fig. 162.—Semidiagrammatic section through the right ear (Czermak). *M,* concha; *G,* external auditory meatus; *T,* tympanic membrane; *P,* tympanic cavity; *o,* oval foramen; *r,* round foramen; *R,* pharyngeal opening of Eustachian tube; *V,* vestibule; *B,* a semicircular canal; *S,* the cochlea; *Vt,* scala vestibuli; *Pt,* scala tympani; *A,* auditory nerve.

This passage is closed at its inner end by the *tympanic* or *drum membrane, T.* It is lined by skin, through which numerous small glands, secreting the *wax* of the ear, open.

The Tympanum (*P,* Fig. 162) is an irregular cavity in the temporal bone, closed externally by the drum membrane.

From its inner side the *Eustachian tube* (*R*) proceeds to the pharynx, and the mucous membrane of that cavity is continued up the tube to line the tympanum; the proper tympanic membrane composed of connective tissue is therefore covered by mucous membrane on its inner, as it is by very thin skin on its outer, side. In the bony inner wall of the tympanum are two small apertures, the *oval* and *round foramens, o* and *r,* which lead into the labyrinth. During life the round aperture is closed by the lining mucous membrane, and the oval in another way, to be described presently. The *tympanic membrane, T,* stretched across the outer side of the tympanum, forms a shallow funnel with its concavity outwards. It is pressed by the external air on its exterior, and by air entering the tympanic cavity through the Eustachian tube on its inner side. If the tympanum were closed the pressures on the inner and outer sides of the drum membrane would not be always equal when barometric pressure varied, and the membrane would be bulged in or out according as the external or internal pressure on it were the greater. On the other hand, were the Eustachian tube always open the sounds of our own voices would be loud and disconcerting, so it is usually closed; but every time we swallow it is opened, and thus the air-pressure in the cavity is kept equal to that in the external auditory meatus. By holding the nose, keeping the mouth shut, and forcibly expiring, air may be forced under pressure into the tympanum, and will be held in part imprisoned there until the next act of swallowing. On making a balloon ascent or going rapidly down a deep mine, the sudden and great change of aërial pressure outside frequently causes painful tension of the drum membrane, which may be greatly alleviated by frequent swallowing movements.

The Auditory Ossicles. Three small bones lie in the tympanum forming a chain from the drum membrane to the oval foramen. The external bone (Fig. 163) is the *malleus* or *hammer ;* the middle one, the *incus* or *anvil ;* and the internal, the *stapes* or *stirrup.* The malleus, *M,* has an upper enlargement or *head,* which carries on its inner side an articular surface for the incus; below the head is a constriction, the *neck,* and below this two processes complete the bone; one, the *long* or *slender process,* is imbedded in a ligament which reaches from it to the front wall of the tympanum; the other process, the *handle,*

reaches down between the mucous membrane lining the
inside of the drum membrane
and the membrane proper,
and is firmly attached to the
latter near its centre and keeps
the membrane dragged in there
so as to give it its peculiar
concave form, as seen from
the outside. The incus has a
body and two processes, and is
much like a molar tooth with
two fangs. On its body is an
articular hollow to receive the
head of the malleus; its short
process (*Jb*) is attached by liga-
ment to the back wall of the
tympanum; the long process
(*Jl*) is directed inwards to the

Fig. 163.—The auditory ossicles of the
right ear, seen from the front. *M*, mal-
leus ; *J*, incus ; *S*, stapes ; *Mcp*, head of
the malleus ; *Mc*, neck of ditto ; *Ml*, long
process ; *Mm*, handle; *Jc*, body, *Jb*, short,
and *Jl*, long process of incus; *Jpl*, os
orbiculare ; *Scp*, head of stapes.

stapes; on the tip of this process is a little knob, which rep-
resents a bone (*os orbiculare*) distinct in early life. The
stapes (*S*) is extremely like a stirrup, and its base (the foot-
piece of the stirrup) fits into the oval foramen, to the margin
of which its edge is united by a fibrous membrane, allowing
of a little play in and out.

From the posterior side of the neck of the malleus a liga-
ment passes to the back wall of the tympanum: this, with
the ligament imbedding the slender process and fixed to the
front wall of the tympanum, forms an antero-posterior *axial
ligament*, on which the malleus can slightly rotate, so that the
handle can be pushed in and the head out and *vice versa*.
If a pin be driven through Fig. 163 just below the neck of
the malleus and perpendicular to the paper it will very fairly
represent this axis of rotation. Connected with the malleus
is a tiny muscle, called the *tensor tympani;* it is inserted on
the handle of the bone below the axis of rotation, and when
it contracts pulls the handle in and tightens the drum mem-
brane. Another muscle (the *stapedius*) is inserted into the
outer end of the stapes, and when it contracts fixes the bone
so as to limit its range of movement in and out of the fenestra
ovalis.

The Internal Ear. The labyrinth consists primarily of
chambers and tubes hollowed out in the temporal bone and

inclosed by it on all sides, except for the oval and round foramens on its exterior, and certain apertures on its inner side by which blood-vessels and branches of the auditory nerve enter; during life all these are closed water-tight in one way or another. Lying in the *bony labyrinth* thus consti-

C

A   B

Fig. 164.—Casts of the bony labyrinth. *A,* left labyrinth seen from the outer side ; *B,* right labyrinth from the inner side ; *C,* left labyrinth from above ; *Fr,* round foramen ; *Fv,* oval foramen ; *h,* horizontal semicircular canal ; *ha,* its ampulla ; *vaa,* ampulla of anterior vertical semicircular canal ; *vpa,* ampulla of posterior vertical semicircular canal ; *vc,* conjoined portion of the two vertical canals.

tuted, are membranous parts, of the same general form but smaller, so that between the two a space is left; this is filled with a watery fluid, called the *perilymph;* and the *membranous internal ear* is filled by a similar liquid, the *endolymph.*

The Bony Labyrinth. The bony labyrinth is described in three portions, the *vestibule,* the *semicircular canals,* and the *cochlea ;* casts of its interior are represented from different aspects in Fig. 164. The vestibule is the central part and has on its exterior the oval foramen (*Fv*) into which the base of the stirrup-bone fits. Behind the vestibule are three bony semicircular canals, communicating with the back of the vestibule at each end, and dilated near one end to form an *ampulla* (*vpa, vaa,* and *ha*). The horizontal canal lies in the plane which its name implies, and has its ampulla at the front end. The two other canals lie vertically, the anterior at right angles, and the posterior parallel, to the median antero-posterior vertical plane of the head. Their ampullary ends are turned forwards and open close together into the vestibule; their posterior ends unite (*vc*) and have a common vestibular opening.

The bony cochlea is a tube coiled on itself somewhat like a snail's shell, and lying in front of the vestibule.

The Membranous Labyrinth. The membranous vestibule, lying in the bony, consists of two sacs communicating by a narrow aperture. The posterior is called the *utriculus,* and into it the membranous semicircular canals open. The anterior, called the *sacculus,* communicates by a tube with the membranous cochlea. The membranous semicircular canals much resemble the bony, and each has an ampulla; in most of their extent they are only united by a few irregular connective-tissue bands with the

Fig. 165.—A section through the cochlea in the line of its axis.

periosteum lining the bony canals; but in the ampulla one side of the membranous tube is closely adherent to its bony protector; at this point nerves enter the former. The relations of the membranous to the bony cochlea are more complicated. A section through this part of the auditory apparatus (Fig. 165) shows that its osseous portion consists of a tube wound two and a half times (from left to right in the right ear and *vice versa*) around a central bony axis, the *modiolus.* From the axis a shelf, the *lamina spiralis,* projects and partially subdivides the tube, extending farthest across in its lower coils. Attached to the outer edge of this bony plate is the membranous cochlea (*scala media*), a tube triangular in cross-section and attached by its base to the outer side of the bony cochlear spiral. The spiral lamina and the membranous cochlea thus subdivide the cavity of the bony tube (Fig. 166) into an upper portion, the *scala vestibuli, SV,* and a lower, the *scala tympani, ST.* Between these lie the lamina spiralis (*lso*) and the membranous cochlea (*CC*), the latter being bounded above by the membrane of Reissner (*R*) and below by the basilar membrane (*b*). The free edge of the lamina spiralis is thickened and covered with connective tissue which is hollowed out so as to form a spiral groove (the *sulcus spiralis, ss*) along the whole length of the membranous cochlea. The latter does not extend to the tip of the bony cochlea; above its apex the scala vestibuli and scala tympani join; both are filled with perilymph, and the

former communicates below with the perilymph cavity of the
vestibule, while the scala tympani abuts below on the round
foramen, which, as has already been pointed out, is closed by
a membrane.   The membranous cochlea contains certain
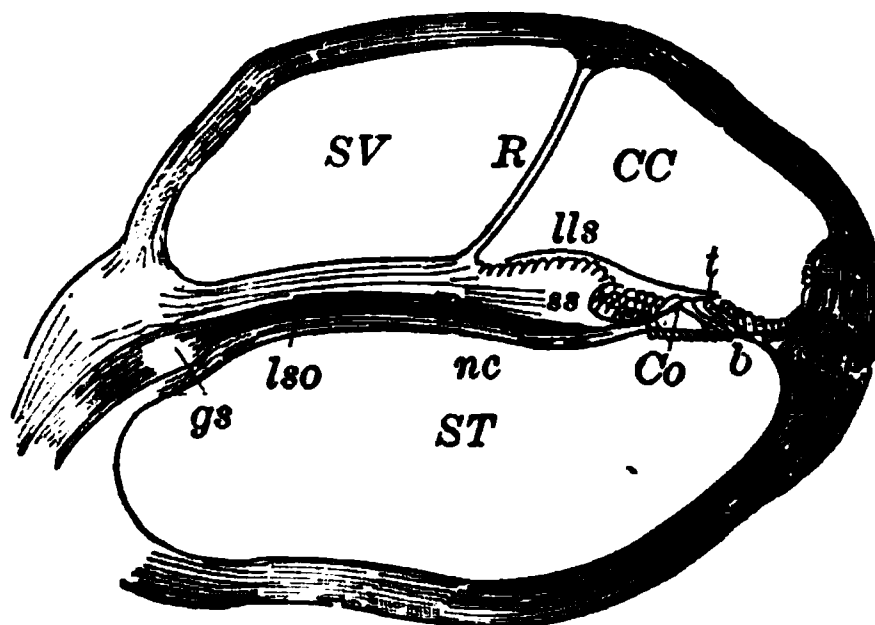
FIG. 166.—Section of one coil of the cochlea, magnified.   *SV, scala vestibuli ;*
R, membrane of Reissner; *CC,* membranous cochlea *(scala media); lls, limbus
laminæ spiralis; t,* tectorial membrane; *ST, scala tympani ;* also, spiral lamina ;
Co, rods of Corti ; *b,* basilar membrane.

solid structures seated on the basilar membrane and forming
the *organ of Corti ;* the rest of its cavity is filled with endo-
lymph, which has free passage to that in the sacculus.

The Organ of Corti.   This contains the end organs of
the cochlear nerves.   Lining the sulcus spiralis are cuboidal
cells; on the inner margin of the basilar membrane the cells
become columnar, and then are succeeded by a row which bear
on their upper ends a set of short stiff hairs, and constitute

A   **B**
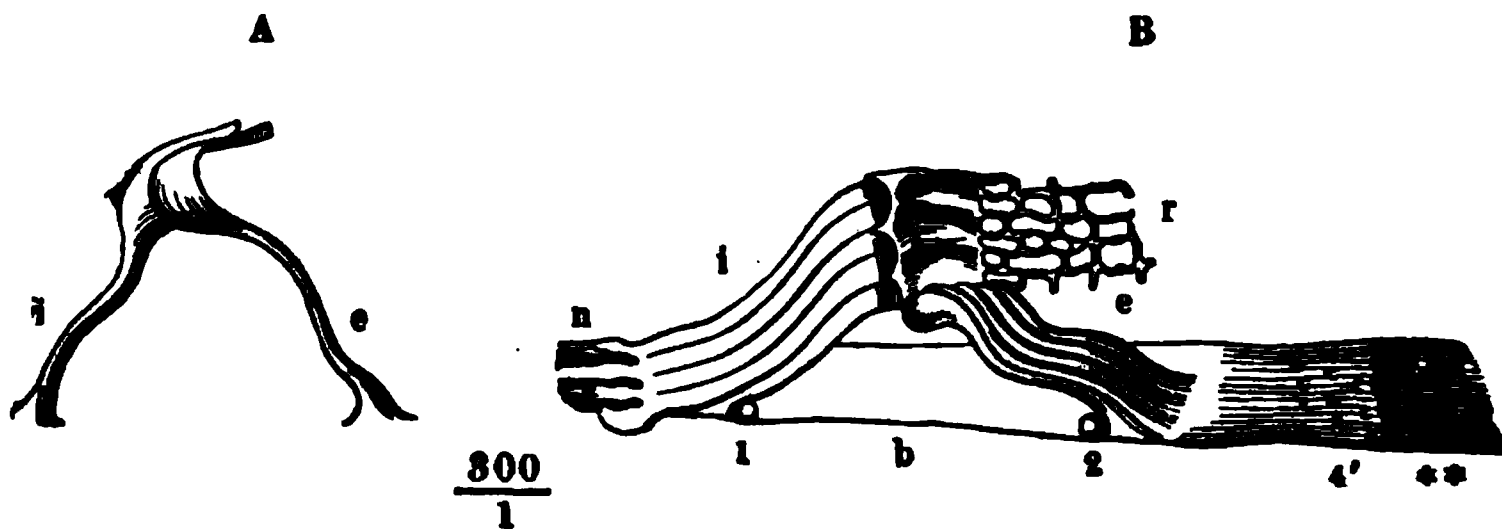
FIG. 167.—The rods of Corti.   *A,* a pair of rods separated from the rest ; *B,* a
bit of the basilar membrane with several rods on it, showing how they cover in
the *tunnel of Corti ; i,* inner, and *e,* outer rods ; *b,* basilar membrane ; *r,* reticular
membrane.

the *inner hair-cells,* which are fixed below by a narrow apex
to the basilar membrane ; nerve-fibres enter them.   To the
inner hair-cells succeed the *rods of Corti (Co,* Fig. 166),
which are represented much magnified in Fig. 167.   These
rods are stiff and arranged side by side in two rows, leaned

against one another by their upper ends so as to cover in a tunnel; they are known respectively as the *inner* and *outer rods*, the former being nearer the *lamina spiralis*. Each has a somewhat dilated base, firmly fixed to the basilar membrane; an expanded head where it meets its fellow (the inner rod presenting there a concavity into which the rounded head of the outer fits); and a slender shaft uniting the two, slightly curved like an italic *f*. The inner rods are more slender and more numerous than the outer, the numbers being about 6000 and 4500 respectively. Attached to the external sides of the head of the outer rods is the *reticular membrane* (*r*, Fig. 167), which is stiff and perforated by holes. External to the outer rods come four rows of *outer hair-cells*, connected like the inner row with nerve-fibres; their bristles project into the holes of the reticular membrane. Beyond the outer hair-cells is ordinary columnar epithelium, which passes gradually into cuboidal cells lining most of the membranous cochlea. The upper lip of the sulcus spiralis is uncovered by epithelium, and is known as the *limbus laminæ spiralis;* from it projects the *tectorial membrane* (*t*, Fig. 166) which extends over the rods of Corti and the hair-cells.

Nerve-Endings in the Semicircular Canals and the Vestibule. Medullated fibres (*f*, Fig. 168) from the vestibular branch of the auditory nerve are distributed along a line across the ampulla of each semicircular canal. They lose their medullary sheath close to the basement membrane, *a*, which the axis cylinders pierce. The axis cylinders branch among the epithelium cells, which at this place are several rows thick, but have not yet been traced into direct continuity with any of them. The cells of the epithelium are of two varieties. The *columnar cells* or *hair cells, c,* do not reach the basement membrane, are nucleated or slightly granular: from the free end of each projects a rigid

FIG. 168.—Diagram of epithelium in nervous region of ampulla of a semicircular canal.

hair process, *d.* The remaining cells, *rod cells, b,* are in several rows: each has a slender inner process extending to the basement membrane and an outer which reaches to the bases of the columnar cells and appears there to end in a rigid membrane, *e,* which is perforated for the passage of the hairs. They probably are mere supporting structures answering somewhat to the fibres of Müller of the retina. After death the hairs tend to break up into a bunch of filaments, and they are found imbedded in a sticky mucus-like material, which is probably a post-mortem product: it has been named the *cupula terminalis.* In some parts of the utricle and saccule is a region of epithelium very similar to that above described, and also supplied with nerve-fibres. In connection with them are found minute calcareous particles, —*otoliths* or ear-stones.

The Loudness, Pitch, and Timbre of Sounds. Sounds, as sensations, fall into two groups—*notes* and *noises.* Physically, sounds consist of vibrations, and these, under most circumstances, when they first reach our auditory organs, are alternating rarefactions and condensations of the air, or *aërial waves.* When the waves follow one another uniformly, or *periodically,* the resulting sensation (if any) is a note; when the vibrations are aperiodic it is a noise. In notes we recognize (1) loudness or intensity; (2) pitch; (3) quality or *timbre,* or, as it has been called, *tone color;* a note of a given loudness and pitch produced by a flute and by a violin has a different character or individuality in each case; this quality is its *timbre.* Before understanding the working of the auditory mechanism we must get some idea of the physical qualities in objective sound of which the subjective differences of auditory sensations are signs.

The *loudness* of a sound depends on the force of the aërial waves; the greater the intensity of the alternating condensations and rarefactions of these in the external auditory meatus, the louder the sound. The *pitch* of a note depends on the length of the waves, that is the distance from one point of greatest condensation to the next, or (what amounts to the same thing) on the number of waves reaching the ear in given time, say a second. The shorter the waves the more rapidly they follow one another, and the higher the pitch of the note. When audible vibrations bear the ratio 1:2 to one another, we hear the musical interval called an

octave. The note *c* on the unaccented octave is due to 132 vibrations in a second. The note *c'*, the next higher octave of this, is produced by 264 vibrations in a second; the next lower octave (great octave, C), by 66; and so on. Sound vibrations may be too rapid or too slow in succession to produce sonorous sensations, just as the ultra-violet and ultra-red rays of the solar spectrum fail to excite the retina. The highest-pitched audible note answers to about 38,016 vibrations in a second, but it differs in individuals; many persons cannot hear the cry of a bat nor the chirp of a cricket, which lie near this upper audible limit. On the other hand, sounds of vibrational rate about 40 per second are not well heard, and a little below this become inaudible. The highest note used in orchestras is the d^v of the fifth accented octave, produced by the piccolo flute, due to 4752 vibrations in a second; and the lowest-pitched is the $E_{,,}$ of the contra octave, produced by the double bass. Modern grand pianos and organs go down to C, in the contra octave (33 vibrations per second) or even A'', (27½), but the musical quality of such notes is imperfect; they produce rather a " hum " than a true tone sensation, and are only used along with notes of higher octaves to which they give a character of greater depth.

Pendular Vibrations. Since the loudness of a tone depends on the vibrational amplitude of its physical antecedent, and its pitch on the vibrational rate, we have still to seek the cause of *timbre;* the quality by which we recognize the human voice, the violin, the piano, and the flute, even when all sound the same note and of the same loudness. The only quality of periodic vibrations left to account for this, is what we may call *wave-form.* Think of the movement of a pendulum; starting slowly from its highest point, it sweeps faster and faster to its lowest, and then slower and slower to its highest point on the opposite side; and then repeats the movements in the reverse direction. Graphically we may represent such vibrations by the outer continuous curved line in Fig. 169. Suppose the lower end of the pendulum to bear a writing point which marked on a sheet of paper travelling down uniformly behind it, and at such a rate as to travel the distance 0-1 in two seconds. If the pendulum were at rest the straight vertical line would be drawn. But if the pendulum were swinging we would get a curved line, compounded of the vertical movement of the paper and

the to-and-fro movement of the pendulum, writing sometimes on one side of the line 0-1-2 and sometimes on the other. Starting at a moment when the pendulum crosses the middle, 0, we would get described the curve 0, $a_1a_2a_3$, at first separating fast from the vertical line, then slower, then returning, at first gradually, then faster, until it crossed the vertical again at the end of a second, and commenced a similar excursion on its other side, at the end of which it would be back at 1, and in just the same position, and ready to repeat exactly the swing, with which we commenced. A pendulum thus executes similar movements in equal periods of time, or its vibrations are *periodic.* A full swing on each side of the position of rest constitutes a complete vibration, so the vibrational period of a seconds pendulum is two seconds: at the end of that time it is precisely where it was two seconds before, and moving in the same direction and at the same rate. It is clear that by examining such a curve we could tell exactly how the pendulum moved, and also in what period, if we knew the rate at which the paper on which its point wrote was moving. The vertical line 0-1-2 is called the *abscissa;* perpendiculars drawn from it and meeting the curve are *ordinates:* equal lengths on the abscissa represent equal times; where an ordinate from a given point of the abscissa meets the curve, there the writing point was at that moment; where successive ordinates increase or decrease rapidly the pendulum moved fast from or towards its position of rest, and *vice versa.* Similarly, any other periodic movement may be perfectly represented by curves; and since the form of the curve tells us all about the movement, it is
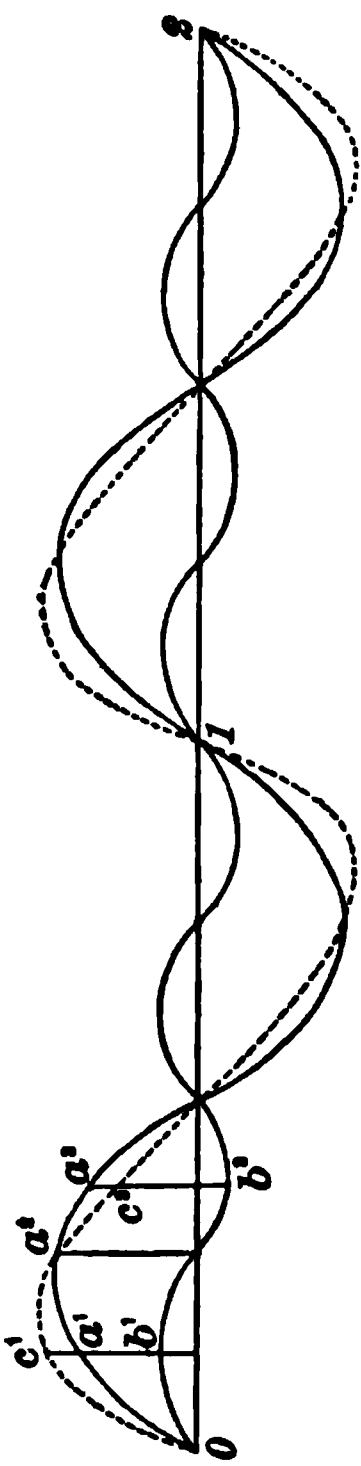
Fig. 169.

common to speak of the "form of a vibration," meaning the form of the curve which indicates its characters. Periodic vibrations (Fig. 169), whose ordinates at first grow fast, then more slowly, next diminish slowly and then faster, and represented by a symmetrical curve on one side the abscissa,

which is repeated exactly on the other side of the abscissa, are known as pendular vibrations.

The Composition of Vibrations. The vibrations of a seconds pendulum set the air-particles in contact with it in similar movement, but the aërial waves succeed one another too slowly to produce in us the sensation of a musical note. If, for the pendulum, we substitute a tuning-fork (the prongs of which move in a like way), and the fork vibrates 132 times per 1″, then 132 aërial waves will fall on the tympanic membrane in that time, and we will hear the note *c* of the unaccented octave. If the larger continuous curve in Fig. 169 represent the aërial vibrations in this case, the distance 0 to 1 on the abscissa will represent $\frac{1}{132}$ of a second. Let, simultaneously, the air be set in movement by a fork of the next higher octave, *c'*, making 264 vibrations per 1″; under the influence of this second fork alone, the aërial particles would move as represented by the line 0, *b'*, *b'*, and so on, the waves being half as long and cutting the abscissa twice as often. But when both forks act together the aërial movement will be the algebraic sum of the movements due to each fork; when both drive the air one way they will reinforce one another, and *vice versa;* the result will be the movement represented by the dotted line, which is still periodic, repeating itself at equal intervals of time, but no longer *pendular*, since it is not alike on the ascending and descending limbs of the curves. We thus get at the fact that non-pendular vibrations may be produced by the fusion of pendular, or, in technical phrase, by their *composition.*

Suppose several musical instruments, as those of an orchestra, to be sounded together. Each produces its own effect on the air-particles, whose movements, being the algebraical sum of those due to all, must at any given instant be very complex; yet the ear can pick out at will and follow the tones of any one instrument. From the complex aërial movement it can select that fraction of it which one vibrating body produces. The air in the external auditory meatus at any given moment can only be in one state of rarefaction or condensation and at one rate and in one direction of movement, this being the resultant of all the forces acting upon it; all clashing, and some pushing one way and others another. If the resultant movement be not periodic it will be

recognized as due to noises or to several simultaneous inharmonic musical tones; this is commonly the case when musical tones are not united designedly, and the ear thus gets one criterion for distinguishing movements of the air due to several simultaneous musical tones. However, a composite set of tones will give rise to periodic vibrations when all are due to vibrations of rates which are multiples of the same whole number. In such cases the movement of the air in the auditory meatus has no property except vibrational form by which the ear could distinguish it from a simple tone; when the two tuning-forks giving the forms of vibration (with rates as 1 to 2), represented in Fig. 169 by continuous lines, are sounded together, we get the new form of vibration represented by the dotted line, and this has the same period as that of the lower-pitched fork; yet the ear can clearly distinguish the resultant sound from that of this fork alone, as a note of the same pitch but of different timbre; and with practice can recognize exactly what simple vibrations go to make it up.

The Analysis of Non-Pendular Vibrations. If a person with a trained ear listens attentively to any ordinary musical tone, such as that of a piano, he hears, not only the note whose vibrational rate determines the pitch of the tone as a whole, but a whole series of higher notes, in harmony with the general or *fundamental tone;* this latter is the *primary partial tone,* and the others are *secondary partial tones;* nearly all tones used in music contain both. If the prime tone be due to 132 vibrations a second (*c*), its first upper partial is *c'* (= 264 vibrations per second); the next is the fifth of this octave (*g'* = 396 = 132 × 3 vibrations per 1′); the next is the second octave, *c''* (132×4 = 528 vibrations per 1′); the next is the major third of the *c''* (= 132 × 5 = 660 vibrations per second = *e''*), and so on. The only form of vibration which gives no upper partial tones is the pendular; we may call notes due to such vibrations *simple tones;* and we, consequently, recognize in music tones which are simple (such as those of tuning-forks) and those which are compound; these latter are non-pendular in form.

We find, then, that the form of aërial vibrations determines in our sensations the occurrence or non-occurrence of upper partial tones. It also, as we have seen, determines the quality or *timbre* of the tone, since vibrational amplitude and

rate are otherwise accounted for in sensation by loudness and pitch.

It can be proved, by the employment of the higher mathematics, that every periodic non-pendular movement can be analyzed (as the dotted curve of Fig. 169 may be) into a given number of pendular vibrations, that is, every compound vibration into a set of simple ones; and that every periodic non-pendular vibration can be made by the combination of pendular. Moreover, any given compound vibration can be analyzed into but one set of simple ones; no other combination will produce it. Consequently a vibrational movement of the air in the external auditory passage, producing a compound musical tone sensation, can be exhibited in every case, but only in one way, as the sum of a number of simple vibrations, whose rates are multiples of that which determines the pitch of the tone.

Now when the trained ear listens to a tone with the object of detecting upper partials if present, it hears them only when the vibrations producing the tone are non-pendular, *i.e.* when upper partials, theoretically, might be expected; and those heard are exactly those demanded by theory; by the help of instruments their detection is made easy even to untrained ears. In ordinary circumstances we do not heed secondary partial tones; we hear a note of the pitch of the primary partial and of a certain timbre; and whenever the upper partials present are different, or of different relative intensities, the timbre of the note varies. Hence it becomes probable that, just as the ear can at will follow any instrument in an orchestra, analyzing the aërial movement so as to select and follow the fraction of the whole due to that one, so it can and does analyze compound tones when proceeding from one instrument, and that the upper partials, not rising into consciousness as definite tones, but present as subdued sensations, give its character to the whole tone and determine its timbre. It might be, however, that the composition of non-pendular vibrations from pendular was a mere mathematical possibility, having no real existence in nature. Before we can accept the above explanation of timbre, we must see if there is any evidence that, as a matter of fact, non-pendular vibrations, not only *may* be, but *are,* made up by the combination of pendular.

Sympathetic Resonance. Imagine slight taps to be

given to a pendulum; if these be repeated at such intervals of time as to always help the swing and never to retard it, the pendulum will soon be set in powerful movement. If the taps are irregular, or when regular come at such intervals as sometimes to promote and sometimes retard the movement, no great swing will be produced; but if they always push the pendulum in the way it is going at that instant, they need not come every swing in order to set up a powerful vibration; once in two, three, or four swings will do. A stretched string, such as that of a piano, is so far like a pendulum that it tends to vibrate at one rate and no other; if aërial waves hit it at exactly the right times they soon set it in sufficiently powerful vibrations to cause it to emit an audible note. By using such strings we might hope to detect the separate pendular vibrations in any non-pendular aërial periodic movement if such really existed; certain strings would pick out the pendular component agreeing in rate with their own vibrational period and be soon set in powerful movement; while those not vibrating in the same period as any of the pendular components, would remain practically at rest, like the pendulum getting taps which sometimes helped and sometimes impeded its swing. If the dampers of a piano be raised and a note be sung loudly to it, it will be found that several strings are set in vibration, such vibrations being called *sympathetic.* The human voice emits compound tones which can be mathematically analyzed into simple vibrations, and if the piano strings set in movement by it be examined, they will be found to be exactly those which answer to these pendular vibrations and to no others. We thus get experimental grounds for believing that compound tones are really made up of a number of simple vibrations, and get an additional justification for the supposition that in the ear each note is analyzed into its pendular components; and that the difference of sensation which we call timbre is due to the effect of the secondary partial tones thus perceived. If so, the ear must have in it an apparatus adapted for *sympathetic resonance.*

It may be asked why, if the ear analyzes vibrations in this way, do we not commonly perceive it ? How is it that what we ordinarily hear is the timbre of a given tone and not

the separate upper partials which give it this character? The explanation is more psychological than physiological, and belongs to the same category as the reason why we do not ordinarily notice the blind spot in the eye, or the doubleness of objects out of the horopter, or the duplicity of stereoscopic images. We only use our senses in daily life when they can tell us something that may be useful to us, and we neglect so habitually all sensations which would be useless or confusing, that at last it needs special attention to observe them at all. The way in which tones are combined to give timbre to a note is a matter of no importance in the daily use of them, and so we fail entirely to observe the components and note only the resultant, until we make a careful and scientific examination of our sensations.

The Functions of the Tympanic Membrane. If a stretched membrane, such as a drum-head, be struck, it will be thrown into periodic vibration and emit for a time a note of a determined pitch. The smaller the membrane and the tighter it is stretched the higher the pitch of its note; every stretched membrane thus has a rate of its own at which it tends to vibrate, just as a piano or violin string has. When a note is sounded in the air near such a membrane, the alternating waves of aërial condensation and rarefaction will move it; and if the waves succeed at the vibrational rate of the membrane the latter will be set in powerful *sympathetic vibration;* if they do not push the membrane at the proper times, their effects will neutralize one another: hence such membranes respond well to only one note. The tympanic membrane, however, responds equally well to a large number of notes; at the least for those due to aërial vibrations of rates from 60 to 4000 per second, running over eight octaves and constituting those commonly used in music. This faculty depends on two things: (1) the membrane is comparatively loosely and not uniformly stretched; (2) it is *loaded* by the tympanic bones.

The drum-membrane is a shallow funnel with its sides convex towards the external auditory meatus; something like an umbrella turned inside out; in such a membrane the tension is not uniform but increases towards the centre, and it has accordingly no proper note of its own. Further, whatever tendency such a membrane may have to vibrate rather at one rate than

another, is almost completely removed by "damping" it; *i.e.* placing in contact with it something comparatively heavy and which has to be moved when the membrane vibrates. This is effected by the tympanic bones, fixed to the drum-membrane by the handle of the malleus. Another advantage is gained by the damping; once a stretched membrane is set vibrating it continues so doing for some time; but if loaded its movements cease almost as soon as the moving impulses. The dampers of a piano are for this purpose; and violin-players have to "damp" with the fingers the strings they have used when they wish the note to cease. The tympanic bones act as dampers.

Functions of the Auditory Ossicles. When the air in the external auditory meatus is condensed it pushes in the handle of the malleus. This bone then slightly rotates on the axial ligament and, locking into the incus where the two bones articulate, causes the long process (*Jl*, Fig. 163) of the latter to move inwards. The incus thus pushes-in the stapes; the reverse occurs when air in the auditory passage is rarefied. Aërial vibrations thus set the chain of bones swinging, and push in and pull out the base of the stapes, which sets up waves in the perilymph of the labyrinth, and these are transmitted through the membranous labyrinth to the endolymph. These liquids being chiefly water, and practically incompressible, the end of the stapes could not work in and out at the oval foramen, were the labyrinth elsewhere completely surrounded by bone: but the membrane covering the round foramen bulges out when the base of the stapes is pushed in, and *vice versa ;* and so allows of waves being set up in the labyrinthic liquids. These correspond in period and form to those in the auditory meatus; their amplitude is determined by the extent of the vibrations of the drum membrane.

The form of the tympanic membrane causes it to transmit to its centre, where the malleus is attached, vibrations of its lateral parts in diminished amplitude but increased power; so that the tympanic bones are pushed only a little way but with considerable force. Its area, too, is about twenty times as great as that of the oval foramen, so that force collected on the large area is, by pushing the tympanic bones, all concentrated on the smaller. The ossicles also form a bent lever (Fig. 163) of which the fulcrum is at the axial ligament and

the effective outer arm of this lever is about half as long again as the inner, and so the movements transmitted by the drum-membrane to the handle of the malleus are communicated with diminished range, but increased power, to the base of the stapes.

Ordinarily, sound-waves reach the labyrinth through the tympanum, but they may also be transmitted through the bones of the head; if the handle of a vibrating tuning-fork be placed on the vertex, the sounds heard by the person experimented upon seem to have their origin inside his own cranium. Similarly, when a vibrating body is held between the teeth, sound reaches the end organs of the auditory nerve through the skull-bones; and persons who are deaf from disease or injury of the tympanum can thus be made to hear, as with the *audiphone.* Of course if deafness be due to disease of the proper nervous auditory apparatus no device can make the person hear.

Function of the Cochlea. We have already seen reason to believe that in the ear there is an apparatus adapted for sympathetic resonance, by which we recognize different musical tone-colors; the minute structure of the membranous cochlea is such as to lead us to look for it there. An old view was that the rods of Corti, which vary in length, were like so many piano-strings, each tending to vibrate at a given rate and picking out and responding to pendular aërial vibrations of its own period, and exciting a nerve which gave rise to a particular tone sensation. When the labyrinthic fluids were set in non-pendular vibrations, the rods of Corti were thought to analyze these into their pendular components, all rods of the vibrational rate of these being set in sympathetic movement, but that rod most whose period was that of the primary partial tone; this rod would determine the pitch of the note, and the less-marked sensation due to the others affected would give the timbre. The rods, however, do not differ in size sufficiently to account for the range of notes which we hear; they are absent in birds, which undoubtedly distinguish different musical notes; and the nerve-fibres of the cochlea are not connected with them but with the hair-cells.

On the whole it seems probable that the basilar membrane is to be looked upon as the primary arrangement for sympathetic resonance in the ear. It increases in breadth twelve times from the base of the cochlea to its tip (the less width of

the lamina spiralis at the apex more than compensating for the less size of the bony tube there) and is stretched tight across, but loosely in the other direction. A membrane so stretched behaves as a set of separate strings placed side by side, somewhat as those of a harp but much closer together; and each string would vibrate at its own period without influencing much those on each side of it. Probably, then, each transverse band vibrates to simple tones of its own period, and excites the hair-cells which lie on it, and through them the nerve-fibres. Perhaps the rods of Corti, being stiff, and carrying the reticular membrane, rub that against the upper ends of the hair-cells which project into its apertures and so help in a subsiduary way, each pair of rods being especially moved when the band of basilar membrane carrying it is set in vibration. The tectorial membrane is probably a "damper;" it is soft and inelastic, and suppresses the vibrations as soon as the moving force ceases.

Function of the Vestibule and Semicircular Canals. Many noises are merely spoiled music; they are due to tones so combined as not to give rise to periodic vibrations; these are probably heard by the cochlea. If a single violent air-wave ever cause a sound sensation (which is doubtful, since any violent push of an elastic substance, such as the air, will cause it to make several rebounds before coming to rest) we perhaps hear it by the vestibule; the otoliths, there in contact with the auditory hairs, are imbedded in a tenacious gummy mass quite distinct from the proper endolymph, and are not adapted for executing regular vibrations, but they might yield to a single powerful impulse and transmit it to the hair-cells, and through them stimulate the nerves. There is reason to believe that the semicircular canals have nothing to do with hearing; their supposed function is described in Chapter XXXVI.

Auditory Perceptions. Sounds, as a general rule, do not seem to us to originate within the auditory apparatus; we refer them to an external source, and to a certain extent can judge the *distance* and *direction* of this. As already mentioned, the extrinsic reference of sounds which reach the labyrinth through the general skull-bones instead of through the tympanic chain is imperfect or absent. The recognition of the distance of a sounding body is possible only when the sound is well known, and then not very accurately; from its

faintness or loudness we may make in some cases a pretty good guess. Judgments as to the direction of a sound are also liable to be grossly wrong, as most persons have experienced. However, when a sound is heard louder by the left than the right ear we can recognize that its source is on the left; when equally with both ears, that it is straight in front or behind; and so on. The concha has perhaps something to do with enabling us to detect whether a sound originates before or behind the ear, since it collects, and turns with more intensity into the external auditory meatus, sound-waves coming from the front. By turning the head and noting the accompanying changes of sensation in each ear we can localize sounds better than if the head be kept motionless. The large movable concha of many animals, as a rabbit or a horse, which can he turned in several directions, is probably an important aid to them in detecting the position of the source of a sound. That the recognition of the direction of sounds is not a true sensation, but a judgment, founded on experience, is illustrated by the fact that we can estimate much more accurately the direction of the human voice, which we hear and heed most, than that of any other sound.

CHAPTER XXXV.

TOUCH. TEMPERATURE SENSATIONS. PAIN. COMMON SENSATIONS. SMELL. TASTE. THE MUSCULAR SENSE.

The skin is very abundantly supplied with afferent nerve-fibres, and from it we get several very distinct kinds of sensations; it is therefore not surprising that nerve-fibres are found to end in it in different ways, but at present we are not able to associate satisfactorily any one particular variety of cutaneous nerve-ending with the origination of the impulses which lead to the occurrence of any one kind of the skin sensations.

Many cutaneous afferent nerve-fibres end in a very simple way: they form plexuses in the outermost layer of the dermis and then, losing the medullary sheath, the axis cylinders enter the epidermis and there break up into extremely minute filaments which ramify among the cells of the Malpighian layer and terminate there without any special end organs. Other fibres have special terminal apparatuses, known as (1) tactile cells; (2) end bulbs ; (3) tactile corpuscles ; (4) Pacinian bodies.

The Tactile Cells lie usually in the deepest layer of the epidermis, but sometimes are found also in the dermis. They are larger and more granular than the neighboring epidermic cells, more oval, and stain more deeply with some reagents, especially gold chloride. Minute axis-cylinder branches can be traced into close relation to them, and according to some histologists end in flat expansions closely applied to the tactile cells, while others believe the nerve-filament to be directly continuous with the cell substance. These cells are especially abundant in the epidermis lining the root-sheaths of such tactile hairs as the " whiskers " of a cat, but they exist in many if not most regions of the human skin.

The End Bulbs lie in the dermis of certain regions as the lips, but they are mainly confined to the conjunctiva and to the mucous membrane lining the mouth and that of the lowest

part of the rectum, all of which possess tactile sensibility. Very similar bodies are found in the synovial membranes of some joints. In man they are spheroidal and vary in diameter from .03 to 0.1 m.m. ($\frac{1}{850}$–$\frac{1}{250}$ inch). Each has an external *capsule* of connective tissue within which is a *core* consisting of polygonal nucleated ill-defined cells. The nerve-fibre loses its medullary sheath close to the end bulb and the axis cylinder enters the core and there usually breaks up into filaments which ramify between the cells of the core and end in little knobs: sometimes the axis cylinder does not branch.

The tactile corpuscles (Fig. 170) are found especially in the

Fig. 170.—Section of skin showing two papillæ of the dermis and some of the deeper cells of the epidermis ; a, papilla containing blood vessels; b, papilla containing a tactile corpuscle, t ; d, medullated nerve-fibres going to the corpuscle; at f, optical cross-sections of the fibres are seen as they wind round the outside of the corpuscle; the general transverse direction of the connective-tissue bundles of the capsule of the corpuscle is shown.

skin of the hands and feet, but also on the inner surface of the forearm, on the nipple, the lips, and mucous membrane of the tip of the tongue. They lie in dermic papillæ and are oval in form, measuring about 0.8 m.m. ($\frac{1}{300}$ inch) in the long and 0.3 m.m. ($\frac{1}{800}$ inch) in the transverse diameter. Each has an outer capsule of connective tissue from which many transverse or oblique dissepiments enter and divide the interior into many small chambers. Two or three medullated nerve-fibres go to each corpuscle, and after winding around it obliquely several times penetrate the capsule at various levels, at the same time becoming non-medullated. The axis cylinders run in the clefts between the connective-tissue dissepiments and after branching many times end in pear-shaped or spherical enlargements, which are always placed near the outside of the corpuscle.

The Pacinian Bodies or Corpuscles (Fig. 171) are found in large numbers in the subcutaneous areolar tissue of the hand and foot, and occasionally in other regions of the skin. But they are also found in internal parts, as on the nerves of tendons and ligaments and on some branches of the solar plexus; and they are very abundant and easily seen in the mesentery of the cat, so that though almost certainly organs in which afferent nerve impulses originate, they are not organs of touch. The corpuscles are oval, often curved on the long axis, and from 1.5 to 2.5 m.m. ($\frac{1}{15}-\frac{1}{10}$ inch) in length. When fresh they have a whitish translucent appearance and are somewhat more opaque in the centre. When magnified each Pacinian body is seen to consist of an almost structureless core surrounded by many concentric capsules. Each capsule is a layer of imperfectly developed connective tissue having a few very fine fibres, the interstices between which are filled with liquid: each surface of each capsule is formed by a well-marked layer of flat nucleated cells, and the cell layer on the inner side of one capsule is separated from the layer on the outer side of the next by a narrow cleft, which is a lymph lacuna. The capsules are usually so closely applied to one another that the lymph spaces between them are almost obliterated. A medullated nerve-fibre runs to one pole of each Pacinian body and the axis cylinder and medullary sheath are continued through the capsules to the core; the medullary sheath becoming thinner on the way. The axis cylinder enters the core and runs to near its opposite end, where it ends in a rounded enlargement or sometimes divides into several short branches, each with a knobbed end.

Fig. 171.—A Pacinian corpuscle, magnified.

Touch, or the Pressure Sense. Through the skin we get several kinds of sensation; touch proper, heat and cold, and pain; and we can with more or less accuracy localize them on the surface of the Body. The interior of the mouth

possesses also these sensibilities. Through touch proper we recognize pressure or traction exerted on the skin, and the force of the pressure; the softness or hardness, roughness or smoothness, of the body producing it; and the form of this, when not too large to be felt all over. When to learn the form of an object we move the hand over it, muscular sensations are combined with proper tactile, and such a combination of the two sensations is frequent; moreover, we rarely touch anything without at the same time getting temperature sensations; therefore pure tactile feelings are rare.

From an evolution point of view, touch is probably the first distinctly differentiated sensation, and this primary position it still largely holds in our mental life; we mainly think of the things about us as objects which would give us certain tactile sensations if we were in contact with them. Though the eye tells us much quicker, and at a greater range, what are the shapes of objects and whether they are smooth, rough, and so on, our real conceptions of round and square and rough bodies are derived through touch, and we largely translate unconsciously the teachings of the eye into mental terms of the tactile sense.

The delicacy of the pressure sense varies on different parts of the skin; it is greatest on the forehead, temples, and back of the forearm, where a weight of 2 milligr. (.03 grain) pressing on an area of 9 sq. millim. (.0139 sq. inch) can be felt. On the front of the forearm 3 milligr. (.036 grain) can be similarly felt, and on the front of the forefinger 5 to 15 milligr. (.07–0.23 grain).

In order that the sense of touch may be excited neighboring skin areas must be differently pressed; when we lay the hand on a table this is secured by the inequalities of the skin, which prevent end organs, lying near together, from being equally compressed. When, however, the hand is immersed in a liquid, as mercury, which fits into all its inequalities and presses with practically the same weight on all neighboring immersed areas, the sense of pressure is only felt at a line along the surface, where the immersed and non-immersed parts of the skin meet.

It was in connection with the tactile sense that the facts on which so-called psycho-physical law (Chap. XXXI.) is based, were first observed. The smallest perceptible difference of pressure recognizable when touch alone is used, is about ⅓;

i.e., we can just tell a weight of 20 grams (310 grains) from one of 30 (465 grains) or of 40 grams (620 grains) from one of 60 (930 grains); the change which can just be recognized being thus the same fraction of that already acting as a stimulus. The ratio only holds good, however, for a certain mean range of pressures; it is not true for very small or very great pressures. The experimental difficulties in determining the question are considerable; muscular sensations must be rigidly excluded; the time elapsing between laying the different weights on the skin must always be equal; the same region and area of the skin must be used; the weights must have the same temperature; and fatigue of the organs must be eliminated. Considerable individual variations are also observed, the least perceptible difference not being the same in all persons.

The Localizing Power of the Skin. When the eyes are closed and a point of the skin is touched we can with some accuracy indicate the region stimulated; although tactile feelings are in general characters alike, they differ in something (*local sign*) besides intensity by which we can distinguish them; some sensation quality must be present enabling us to tell from one another two precisely similar contacts of an external object when applied, say, to the tips of the fore and ring fingers respectively. The accuracy of the localizing power is not nearly so great as in the retina and varies widely in different skin regions; it may be measured by observing the least distance which must separate two objects (as the blunted points of a pair of compasses) in order that they may be felt as two. The following table illustrates some of the differences observed—

Tongue-tip...............................	1.1 mm.	(.04 inch)
Palm side of last phalanx of finger........	2.2 mm.	(.08 inch)
Red part of lips...........................	4.4 mm.	(.16 inch)
Tip of nose...............................	6.6 mm.	(.24 inch)
Back of second phalanx of finger..........	11.0 mm.	(.44 inch)
Heel......................................	22.0 mm.	(.88 inch)
Back of hand..............................	30.8 mm.	(1.23 inches)
Forearm..................................	39.6 mm.	(1.58 inches)
Sternum..................................	44.0 mm.	(1.76 inches)
Back of neck..............................	52.8 mm.	(2.11 inches)
Middle of back............................	66.0 mm.	(2.64 inches)

The localizing power is a little more acute across the long

axis of a limb, and is better when the pressure is only strong enough to just cause a distinct tactile sensation, than when it is more powerful; it is also very readily and rapidly improvable by practice.

It might be thought that this localizing power depended directly on nerve distribution; that each touch nerve had connection with a special brain-centre at one end (the excitation of which caused a sensation with a characteristic local sign), and at the other end was distributed over a certain skin area, and that the larger this area the farther apart might two points be and still give

Fig. 172.

rise to only one sensation. If this were so, however, the peripheral tactile areas (each being determined by the anatomical distribution of a nerve-fibre) must have definite unchangeable limits, which experiment shows that they do not possess. Suppose the small areas in Fig. 172 to each represent a peripheral area of nerve distribution. If any two points in *c* were touched we would according to the theory get but a single sensation; but if, while the compass points remained the same distance apart, or were even approximated, one were placed in *c* and the other on a contiguous area, two fibres would be stimulated and we ought to get two sensations; but such is not the case; on the same skin region the points must be always the same distance apart, no matter how they be shifted, in order to give rise to two just distinguishable sensations.

It is probable that the nerve areas are much smaller than the tactile; and that several unstimulated must intervene between the excited, in order to produce sensations which shall be distinct. If we suppose twelve unexcited nerve areas must intervene, then, in Fig. 172, *a* and *b* will be just on the limits of a single tactile area; and no matter how the points are moved, so long as eleven, or fewer, unexcited areas come between, we would get a single tactile sensation; in this way we can explain the fact that tactile areas have no fixed boundaries in the skin, although the nerve distribution in any part must be constant. We also see why the back of a knife laid on the surface causes a continuous linear sensation, although

it touches many distinct nerve areas; if we could discriminate the excitations of each of these from that of its immediate neighbors we would get the sensation of a series of points touching us, one for each nerve region excited; but in the absence of intervening unexcited nerve areas the sensations are fused together.

The ultimate differentiation of tactile areas takes place in the central organs, as will be more fully pointed out in the next chapter. Afferent nerve impulses reaching the spinal cord from a finger-tip enter the gray matter and tend to spread or radiate in it; from the gray region through which they spread, impulses are sent on to perceptive tactile centres in the brain; if two skin-points are so close that their regions of irradiation in the cord overlap, then the two points touched cannot be discriminated in consciousness, since the brain region excited is in part common to both. The more powerful the stimulus the wider the irradiation in the cord, and hence the less accurate the discriminating power. The more often an impulse has travelled, the more does it tend to keep its own proper tract through the gray matter of the cord, and get on to its own proper brain-centre alone; hence the increase of tactile discrimination with practice, for we cannot suppose it to be due to a growth of more nerve-fibres down to the skin, and a rearrangement of the old, with smaller areas of anatomical distribution. As a general rule, more movable parts have smaller tactile areas; this probably depends on practice, since they are the parts which get the greatest number of different tactile stimulations.

The Temperature Sense. By this we mean our faculty of perceiving cold and warmth; and, with the help of these sensations, of perceiving temperature differences in external objects. Its organ is the whole skin, the mucous membrane of mouth and fauces, pharynx and upper part of gullet, and the entry of the nares. Direct heating or cooling of a sensory nerve may stimulate it and cause pain, but not a true temperature sensation; and the amount of heat or cold requisite is much greater than that necessary when a temperature-perceiving surface is acted upon; hence we must assume the presence of temperature end organs.

In a comfortable room we feel at no part of the Body either heat or cold, although different parts of its surface are

at different temperatures; the fingers and nose being cooler than the trunk which is covered by clothes, and this, in turn, cooler than the interior of the mouth. The temperature which a given region of the temperature organ has (as measured by a thermometer) when it feels neither hot nor cold is its *temperature-sensation zero* for that time, and is not associated with any one objective temperature; for not only, as we have just seen, does it vary in different parts of the organ, but also on the same part from time to time. Whenever a skin region passes with a certain rapidity to a temperature above its sensation zero we feel warmth; and *vice versa :* the sensation is more marked the greater the difference, and the more suddenly it is produced; touching a metallic body, which conducts heat rapidly to or from the skin, causes a more marked hot or cold sensation than touching a worse conductor, as a piece of wood, of the same temperature.

The change of temperature in the organ may be brought about by changes in the circulatory apparatus (more blood flowing through the skin warms it and less leads to its cooling), or by temperature changes in gases, liquids, or solids in contact with it. Sometimes we fail to distinguish clearly whether the cause is external or internal; a person coming in from a windy walk often feels a room uncomfortably warm which is not really so; the exercise has accelerated his circulation and tended to warm his skin, but the moving outer air has rapidly conducted off the extra heat; on entering the house the stationary air there does this less quickly, the skin becomes hotter, and the cause is supposed to be oppressive heat of the room. Hence, frequently, opening of windows and sitting in a draught, with its concomitant risks; whereas keeping quiet for five or ten minutes, until the circulation had returned to its normal rate, would attain the same end without danger.

The acuteness of the temperature sense is greatest at temperatures within a few degrees of 30° C. (86° F.); at these differences of less than .1° C. can be discriminated. As a means of measuring absolute temperatures, however, the skin is very unreliable, on account of the changeability of its sensation zero. We can localize temperature sensations much as tactile, but not so accurately.

Are Touch and Temperature Sensations of Different Modality ? Tactile and temperature feelings are ordinarily so

very different that we can no more compare them than luminous and auditory; and if we accept the modern modified form of the doctrine of specific nerve energies (Chap. XIII), in accordance with which the same sensory fibre when excited always arouses a sensation of the same quality, if any, because it excites the same brain-centre, it is hard to conceive how the same fibre could at one time arouse a tactile, and at another a temperature sensation. It has, however, been maintained that touch and temperature feelings sometimes pass into one another insensibly. If a half dollar cooled to 5° C. (41° F.) be placed on a person's brow, and then two (one on the other) warmed to 37° C. (98.5° F.), he commonly thinks the weight in the two cases is equal; *i.e.*, the temperature difference leads to errors in his pressure judgments. But this does not prove an identity in the sensations; the cold half-dollar may produce contraction of the cutaneous tissues, leading to compression of the tactile end organs, which is mistaken, in mental interpretation, for a heavier pressure. When sensations are combined in other cases, as red and blue-green to produce white, or partial tones to form a compound, we either cannot, or can but with difficulty, recognize the components; in this case the person feels both the cold and pressure distinctly when the half-dollar is laid on him.

In certain cases a person mistakes the contact of a piece of raw cotton with his skin, for the approach of a warm object; this has been taken to prove that touch and temperature feelings graduate into one another. However, the feeble touch of the raw cotton might well be less felt than the increased temperature of the skin, due to diminished radiation when it was covered by this non-conducting substance; and the constancy with which, in the ordinary circumstances of life, we feel and discriminate clearly, on the same skin region at the same time, both temperature and touch sensations, is a strong argument against any transition of one into the other.

Moreover, there is direct evidence that three different apparatuses in the skin or at least differently located apparatuses, are concerned in arousing touch, heat and cold sensations. If a metal point, lightly weighted, be slowly and evenly moved along the skin by clockwork, it gives rise to sensations of touch at some places and if hotter or cooler than the skin to sensations of temperature at others; but never when in contact with one point to more than one sensation. If the

points at which the observed person says I feel touch or I feel cold or I feel heat, be carefully marked on the skin and the experiment repeated on one or more subsequent days the contact points for the three sensations are found to be unchanged. In certain cases of spinal-cord disease, moreover, it has been noticed that tactile sensibility may be lost while temperature sensibility remains; and in others that the capacity of feeling warmth may be nearly or completely lost while cold sensation remains normal. Excluding pain (" abnormal sensation "), we must conclude that there are in the skin three distinct sets of nerve-fibres:—One, when excited, arouses " touch " sensation; a second, " warm " sensation; the third, " cold " sensation.

Pain and Common Sensibility. When the skin is powerfully stimulated by heat, cold or pressure, or is inflamed, we get a new sensation which we call *pain.* This is something quite different from the unpleasantness caused by a dazzling light or a musical discord or a disagreeable odor or taste. We recognize these as being still sight or sound or smell or taste sensations. Pain on the one hand is different from any of the normal skin sensations and, on the other, is recognized in consciousness as often proceeding from diseased internal organs from which normally we get no noticeable sensations. An exposed healthy tendon is quite insensible to touch, but if it be inflamed the slightest pressure may give rise to nerve impulses causing very acute pain, and pain which to the consciousness is similar to cutaneous pains or pains of other organs. Since direct stimulation of the sensory nerves proceeding from the skin in any way except through their end organs gives rise to feelings of pain rather than to the special skin sensations, and pressure and temperature feelings do insensibly give way to pain feelings when the stimuli applied to the skin are gradually increased, it has been supposed that pain is not due to excitation of a special nerve apparatus of its own, but to over-excitation of the tactile apparatus. On this theory it would be hard to account for the fact that skin pain is so very different in modality from a touch or temperature feeling, and to understand why it gives rise in consciousness to conceptions concerning a condition of the Body and not of some external object: it is not extrinsically referred by the mind to a quality of anything but the painful part itself, as a dazzling light sensation or a fetid odor is. There is also

experimental and pathological evidence that the paths taken in the spinal cord by nerve impulses causing pain are different from those leading to a consciousness of touch. If certain parts of the cord are cut in the thoracic region of a rabbit, gentle touches on the hind limb appear to be felt; the animal erects its ears or moves its head: but powerful stimulation of the sciatic nerve causes no signs of pain, while if the posterior white columns be cut the animal still can feel stimuli applied to the hind limb and sufficient to cause pain under normal conditions, but it appears insensible to gentle pressure on the skin. In human beings very similar phenomena have been observed in cases of spinal-cord disease: and in a certain stage of chloroform or ether narcosis the patient feels the surgeon's hand or his knife where it touches the skin, but he experiences no pain when deeper parts are cut.

Such considerations seem to lead to the conclusion that the nerve-fibres and sense apparatuses concerned with painful sensations are quite distinct from those of all the special senses. If that be so we must also assume that there are " pain " fibres very widely distributed over the skin and through most other parts of the Body, and usually not so stimulated as to cause sensations which are present in consciousness. In accident or disease the afferent impulses become powerful enough to arouse perception and imperiously call attention to danger. The nerve-fibres concerned may be named " fibres of common sensibility," and there is reason to believe that, normally, feeble afferent impulses travel along them from nearly all organs to the fore brain; but so weak and so uniform as not to excite a perceived feeling: these impulses would thus form a great background of subconscious feeling, on which special points from time to time become conspicuous as one or other nerve of special sense is stimulated or some fibre of common sensibility is abnormally excited. So far as the epidermis is concerned, the axis-cylinder branches, which end in it without any special terminal apparatus, may be specially fibres of common sensibility.

Pains can be localized though but only imperfectly, and the less perfectly the more severe they are. The exact place of a needle prick after removal of the needle (so that there is no guiding concomitant touch sensation) cannot be recognized as well as pin touch on the same region of the skin, but still fairly well; while the acute pain caused by a small abscess

(bone felon) under the periosteum of a finger bone is often felt all over the forearm; and a single diseased tooth may cause pain felt over the whole of that side of the face. This is probably due to imperfection in brain and spinal cord of the isolation of the paths of conduction of the nervous impulses concerned.

Common Sensations. These agree with pain sensations in calling attention to conditions of our Bodies and not of outer things. Some of them, as general *malaise* and "feeling well," are probably due to modifications of the general inflow of impulses through the apparatus of common sensibility, not sufficient to cause a feeling of definite pain or pleasure. Others, as hunger, thirst and nausea, may have similar origin, but in a more localized region.

Hunger and Thirst. These sensations, which regulate the taking of food, are peripherally localized in consciousness, the former in the stomach and the latter in the throat, and local conditions no doubt play a part in their production; though general states of the Body are also concerned.

Hunger in its first stages is probably due to a condition of the gastric mucous membrane which comes on when the stomach has been empty some time, and it may be temporarily stilled by filling the organ with indigestible substances. But soon the feeling comes back intensified and can only be allayed by the ingestion of nutritive substances; provided these are absorbed and reach the blood, their mode of entry is unessential; the hunger may be stayed by injections of food into the rectum as well as by putting it into the stomach.

Similarly, thirst may be temporarily relieved by moistening the throat without swallowing, but then soon returns; while it may be permanently relieved by water injections into the veins, without wetting the throat.

While both sensations depend in part on local peripheral conditions, they may also be, and more powerfully, excited by poverty of the blood in foods and water; such deficiency probably directly stimulates hunger and thirst brain-centres.

Smell. The region of the nostril nearest its outer end possesses the sense of touch, and most of its lining mucous membrane has common sensibility, which can be aroused by such substances as ammonia vapor: the nerve-fibres concerned in these feelings are derived from the superior maxillary branch of the fifth nerve.

The olfactory organ proper consists of the upper portions of the two nasal cavities, over which the endings of the olfactory nerves are spread and where the mucous membrane has a brownish-yellow color. This region (*regio olfactoria*) covers the upper and lower turbinate bones, which are expansions of the ethmoid on the outer wall of the nostril chamber, the opposite part of the partition between the nares, and the part of the roof of the nose separating it from the cranial cavity. The epithelium covering the mucous membrane contains three varieties of cells (2, Fig. 173). The cells of one set are much like ordinary columnar epithelium, but with long branched processes attached to their deeper ends; mixed with these are peculiar cells, each of which has a large nucleus surrounded by a little protoplasm; a slender external process reaching to the surface; and a very slender deep one. The latter cells have been supposed to be the proper olfactory end organs, and to be connected with the fibres of the olfactory nerve, which enter the deeper strata of the epithelium and there divide. In Amphibia the corresponding cells have fine filaments on their free ends. The cells of the third kind are irregular in form and lie in several rows in the deeper parts of the epithelium. It may be that the cylindrical cells if not (as is possible) directly concerned in olfaction, have important functions in regard to the nourishment of the olfactory cells which they surround; they may for example supply them with needful material, as the pigment-cells of the retina are concerned in the formation of visual purple in the rods.

Fig. 173.—Cells from the olfactory epithelium. 1, from the frog. 2, from man; *a*, columnar cell, with its branched deep process; *b*, so-called olfactory cell; *c*, its narrow outer process; *d*, its slender central process. 3, gray nerve-fibres of the olfactory nerve, seen dividing into fine peripheral branches at *a*.

Odorous substances, the stimuli of the olfactory apparatus, are always gaseous and frequently act powerfully when present in very small amount. We cannot, however, classify them by

the sensations they arouse, or arrange them in series; and smells are but minor sensory factors in our mental life, although very powerful associations of memory are often aroused by odors. We commonly refer them to external objects, since we find that the sensation is intensified by " sniffing " air into the nose, and ceases when the nostrils are closed. Their peripheral localization is, however, imperfect, for we confound many smells with tastes (see below); nor can we well judge of the direction of an odorous body through the olfactory sensations which it arouses.

Taste. The organ of taste is the mucous membrane on the dorsum of the tongue and, in some persons, of the soft palate and fauces. The nerves concerned are the glossopharyngeals, distributed over the hind part of the tongue, and the *lingual branches* of the inferior maxillary division of the trigeminals on its anterior two thirds.

On the tongue most of the sensory nerves run to papillæ; the circumvallate have the richest supply, and on these are peculiar end organs (Fig. 174) known as *taste buds*; they

Fig. 174.—Taste-buds.

are oval and imbedded in the epidermis covering the side of the papilla. Each consists, externally, of a number of flat, fusiform, nucleated cells and, internally, of six or eight so-called *taste-cells*. The latter are much like the olfactory cells of the nose, and are probably connected with nerve-fibres at their deeper ends. The capsule formed by the enveloping cells has a small opening on the surface; each taste-cell terminates in a very fine thread which there protrudes. Taste-buds are also found on some of the fungiform papillæ, and it is possible that simpler structures, not yet recognized, and consisting of single taste-cells are widely spread over the

tongue, since the sense of taste exists where no taste-buds can be found. The filiform papillæ are probably tactile.

That substances be tasted they must be in solution: wipe the tongue dry and put a crystal of sugar on it; no taste will be felt until exuding moisture has dissolved some of the crystal. Excluding the feelings aroused by acid substances, tastes proper may be divided into sweet, bitter, acid, and saline. Although contributing much to the pleasures of life, they are intellectually, like smells, of small value; the perceptions we attain through them as to qualities of external objects being of little use, except as aiding in the selection of food, and for that purpose they are not safe guides at all times.

Many so-called tastes (flavors) are really smells; odoriferous particles of substances which are being eaten reach the olfactory region through the posterior nares and arouse sensations which, since they accompany the presence of objects in the mouth, we take for tastes. Such is the case, *e.g.*, with most spices; when the nasal chambers are blocked or inflamed by a cold in the head, or closed by compressing the nose, the so-called taste of spices is not perceived when they are eaten; all that is felt, when cinnamon, *e.g.*, is chewed under such circumstances is a certain pungency due to its stimulating nerves of common sensation in the tongue. This fact is sometimes taken advantage of in the practice of domestic medicine when a nauseous dose, as rhubarb, is to be given to a child. Tactile sensations play also a part in many so-called tastes.

As the tongue, in addition to taste functions, possesses tactile, temperature, and general sensibility, its nerve apparatus must be complex; and there is even reason to believe that different nerve-fibres with presumably different end organs are concerned in the different true tastes. Most persons taste bitter things better with the back part of the tongue and sweet things with the tip, and in some persons the separation of function is quite complete. Chemical compounds are known which in such persons cause a pure sweet sensation if placed on the tongue tip and a pure bitter sensation if placed in the region of the circumvallate papillæ; these facts seem to show that the fibres concerned in bitter and sweet sensation are distinct. Again, if leaves of a certain plant (*Gymnema sylvestre*) be chewed, the capacity to taste sweet or bitter things is lost for some time, but salts and acids

are tasted as well as usual; and most persons taste salines better at the sides of the tongue than elsewhere; so that the salt and acid sensations seem to have a different apparatus, not only from the sweet and bitter, but from one another.

The Muscular Sense. The muscles are endowed with common sensibility, as proved by the pains of cramp and fatigue, but in connection with them we have other sensations of great importance, although they do not often become so obtrusive in consciousness as to arouse separate attention. Certain of these feelings (*muscle sensations proper*) are due to the excitation of sensory nerves ending within the muscles themselves: others (*innervation sensations*) have possibly a central origin and accompany the starting of volitional impulses from brain-cells; they are only felt in connection with the voluntary skeletal muscles.

We have at any moment a fairly accurate knowledge of the position of various parts of our Bodies, even when we do not see them; and we can also judge fairly accurately the extent of a movement made with the eyes shut. The afferent nerve impulses concerned in the development of such judgments may be various; different parts of the skin are pressed or creased; different joints are subjected to pressure; different tendons are put on the stretch and different muscles are in different states of contraction, and it is by no means easy to determine the part played in each case by the sensory nerves of the different organs. Moreover, when we push against an object, or lift it, we are able to form a judgment as to the amount of effort exerted; but here again pressure on skin and joints and tension of tendons come in. Although under normal circumstances the skin sensations are undoubtedly of importance, they are not necessary: persons with cutaneous paralysis can, apart from sight, judge truly the position of a limb and the extent of movement made by it; and in many movements change in joint pressure must be very little if any. We have then to look to muscles and tendons themselves for an important part of the sensations, and in both muscles and tendons there are organs in connection with nerve-fibres which are certainly sensory in nature: moreover, muscle sensory nerves, whether through the organs of Golgi or some other end organ, appear to be excited by mere passive change of form in the muscle: with the eyes closed each of us can tell how much another person has lifted one of our arms.

Whether, in addition to the true muscle sense, dependent on afferent impulses sent to the brain from the contracted muscle or its tendons, we have a more direct consciousness of the amount of will exerted to produce a given muscular contraction, and can form thereby a judgment as to the extent of the movement or effort, is a question still in dispute. A main argument in favor of the existence of such centrally originating " innervation sensations " is based on phenomena observed in persons afflicted with paresis. They frequently judge erroneously for a time as to the extent of movements made by them, thinking that the movement is greater than it really is. It is argued that in such cases the error cannot be based on peripheral sensations, but must be due to the fact that the person judges by the amount of volitional effort he has made, which was such as in his previous condition of health would have produced a greater muscular contraction than it now does in his paretic condition. It is especially in connection with eye muscles that such errors have been noticed. When we follow a moving object with the eyes we judge of the rate of movement by the degree of contraction of the ocular muscles needed to keep its image on the two foveas: if the eye muscles become suddenly enfeebled the person at first thinks he turns his eyeballs faster than he really does and hence that the object is moving faster than it actually does: or he may not move his eye at all when he has willed to do so, and hence conclude that stationary objects are in motion because their images are still formed on the same region of the retina, which could not be the case with stationary objects if the position of the eyes were changed.

Whether the sensations by which we judge the extent of a muscular movement be entirely peripheral or in part central, they enable us to determine very minute differences of contraction: the ocular determination of the distance of an object not too far off to have its absolute distance determined with considerable accuracy, depends almost entirely upon judgments based upon very small changes in the degree of contraction of the internal and external straight (*recti*) muscles, converging or diverging the eyeballs; and of the ciliary muscle determining the necessary accommodation of the lens. A singer, too, must be able to judge with great minuteness the degree of contraction of the small muscles of the larynx necessary to produce a certain tension of the vocal cords. It may

be well to point out that we do not refer a muscular sensation to any given muscle or muscles: it is merely associated with a certain movement or position, and a person who knows nothing about his ocular muscles can judge distance through sensations derived from them, quite as well as any anatomist. This fact is of course correlated with the fact that in voluntary movement we do not make a conscious effort to contract any particular muscles: the higher nerve centres are merely concerned with the initiation of a given movement of a given extent, and all the details are carried out by lower co-ordinating centres. In ordinary daily life in fact we have no interest whatever in a muscular contraction *per se;* all we are concerned with is the result, and consciousness has never had need to trouble itself, if it could, with associating a particular feeling or a particular movement with any individual muscle.

Muscular feelings are, as already pointed out, frequently and closely combined not only with visual but also with tactile, in providing sensations on which to base judgments: in the dark, when an object is of such size and form that it cannot be felt all over by any one region of the skin, we deduce its shape and extent by combining the tactile feelings it gives rise to, with the muscular feelings accompanying the movements of the hands over it. Even when the eyes are used the sensations attained through them mainly serve as short-cuts which we have learned by experience to interpret, as telling us what tactile and muscular feelings the object seen would give us if felt; and, in regard to distant points, although we have learnt to apply arbitrarily selected standards of measurement, it is probable that distance, in relation to perception, is primarily a judgment as to how much muscular effort would be needed to come into contact with the thing looked at.

When we wish to estimate the weight of an object we always, when possible, lift it, and so combine muscular with tactile sensations. By this means we can form much better judgments. While with touch alone just perceptibly different pressures have the ratio 1 : 3, with the muscular sense added differences of $\frac{1}{17}$ can be perceived.

CHAPTER XXXVI.

THE SPINAL CORD AND REFLEX ACTIONS.

The Special Physiology of Nerve-Centres. We have already studied the general physiological properties of nerves and nerve-centres (Chap. XIII) and found that while the former are mere transmitters of nervous impulses, the latter do much more than merely conduct. In some cases the centres are *automatic*; they originate nerve impulses, as illustrated by the rhythmic impulses starting from the respiratory centre. In other cases a feeble impulse reaching the centre gives rise to a great discharge of energy from it (as when an unexpected noise produces a violent start, due to many impulses sent out from the excited centre to numerous muscles), so that certain centres are *irritable*. Such nerve-centres contain a store of energy-liberating material which only needs a slight disturbance to upset its equilibrium and initiate powerful efferent impulses as the result of one feeble afferent. Further, the impulses thus liberated are *co-ordinated*. When mucus in the larynx tickles the throat and excites afferent nerve impulses, these, reaching a centre, cause discharges along many efferent fibres, so combined in sequence and power as to produce, not a mere aimless spasm, but a cough which clears the passage. In very many cases the excitation of centres, with or without at the same time some of the above phenomena, is associated with *sensations* or other *states of consciousness*.

We have now to study which of these powers is manifested by different parts of the central cerebro-spinal nervous system, and under what circumstances and in what degree: and also some of the phenomena of conduction in spinal cord and brain.

Conduction in the Spinal Cord. The spinal cord, forming (except the slender sympathetic) the only direct communication between the brain and most of the nerves of the Body, was considered by the older physiologists as merely a huge nerve-trunk, into which the various spinal nerves were

collected on their way to the encephalon. It does, it is true, contain the paths for the conduction of all those impulses which, originating in the cerebrum, give rise to voluntary movements of the trunk and limbs; also for all the centrally travelling impulses which give rise to sensations ascribed to those parts; and it is also the path for certain impulses giving rise to involuntary movements as, for example, those which, originating in the respiratory centre, travel to the phrenic and intercostal nerves.

If, however, the cord were merely collected and continued nerve-roots it ought to increase considerably in bulk as it approached the skull, and this it does not do in anything like the required proportion; a histological enumeration also shows that the total number of fibres cut across in a transverse section of the cord in the upper cervical region is far less than the total number of fibres in all the spinal nerve-roots. Most of the root-fibres, in fact, pass at once into the central gray mass and their axis cylinders end in its cells, or lose their individuality by joining its network of cell branches and fine non-medullated fibres. Most of the fibres of the anterior root end in nerve-cells near the level at which they join the cord, especially in the cells of the anterior horns: many of the fibres of the posterior roots also join the gray network, either at or a little above or a little below the level at which they reach the cord, but some appear to run on to the brain without entering the gray core. Those which do pass into it probably break up in its network and are not directly continued into a cell, but this is still uncertain. In correspondence with the fact that most of the spinal nerve-fibres have their primary termination in it near their point of entry, is the fact that the amount of gray matter at any level is greater or less according as the nerve-roots at that level are large or small: the cervical and lumbar enlargements for example are almost entirely due to increase of gray matter in those regions. When we make a voluntary movement of a limb the impulse orginating in the brain does not pass directly to the motor nerves of the muscles concerned, but to a mechanism in the gray matter of the cord, which is in connection with those muscles; and when we feel an object touching the finger, the afferent impulses probably, though not so certainly, first enter the gray core of the cord and thence make a fresh start to the brain. When the blood-vessels constrict on painful stimu-

lation of the sciatic nerve, impulses must travel from the lumbar enlargement of the cord to the vaso-constrictor centre in the medulla and reflex afferent impulses from it down the cord to the region of the gray matter from which the anterior roots conveying motor fibres for the blood-vessels pass out Although part of the whole course of such impulses lies in the gray core, yet most of it, in the normal physiological working of the Body lies, so far as the cord is concerned, in its white columns, and we have now to try and track these paths: as also paths of special conduction between different regions of the spinal gray matter themselves. The gray matter of the cord being directly continuous with the gray matter of the medulla oblongata and through it with that of some other parts of the brain can transmit impulses after all the white columns of the cord have been divided, but with such conduction we are not for the present concerned.

To determine the special paths in the white substance of the cord from and to the brain several methods have been employed. Experiment on animals as to loss of sensation or the power of voluntary movement in parts supplied by nerves arising from the cord posterior to a partial transverse section give on the whole unsatisfactory results: partly because of the difficulty in exactly limiting the section and partly because of the general shock to the nervous system resulting from the operation. Still something has been learned in that way, and something also from observations on persons suffering from more or less localized diseases of the spinal cord. Direct stimulation of parts of the cord exposed by transverse section have also given some results; but more satisfactory evidence as to tracts of conduction between the brain and cord have been obtained by the Wallerian method and by the study of development. Removal or disease of certain parts of the brain and partial cross-sections of portions of it or of the cord itself, give rise to degeneration of localized groups of fibres in parts of the cord posterior to the disease or injury: these are *tracts of descending degeneration.* Partial cross-section of other parts of the cord or of the posterior spinal roots lead to degenerations above the injury or *ascending degenerations:* and in general all the fibres which degenerate as a result of a given injury acquire in embryonic development their medullary sheaths at the same time, which is different from the period at which other groups acquire theirs. Finally,

some regions of the white substance of the cord undergo no degeneration as the result of injuries above or below them.

The details as to the result of sections or injuries at various levels differ considerably, but their broad features are indicated in Fig. 175, in which tracts of descending degeneration

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Fɪɢ. 175.—Diagram of a cross-section of the spinal cord near the upper part of the cervical enlargement to indicate the main tracts of ascending and descending degenerations. The gray matter is in solid black; tracts of descending degeneration are shaded in vertical and of ascending in horizontal lines; *pt*, pyramidal or crossed pyramidal tract; *dpt*, direct pyramidal tract; *dc-al,* descending *antero-lateral tract; ct,* comma tract; *cbt.* cerebellar tract; *ac-al.* ascending antero-lateral tract; *a, e, ɩ, c,* posterior median tract; *il,* tract of Lissauer; *epc,* external posterior column; *i.al* internal antero-lateral column.

are shaded in vertical lines, and of ascending degeneration in black. It represents a cross-section of the cord at about the level of the fifth cervical nerve. The descending area of degeneration, *pt,* is the *pyramidal tract* or *crossed pyramidal tract;* its fibres degenerate posterior to any hemisection of the cord on the same side, and to section of the anterior pyramid of the medulla oblongata, or of the crus cerebri on the opposite side, or as a result of disease or lesions of certain parts of the convolutions of the cerebral hemisphere of the opposite side. This tract is large in the upper part of the cord and becomes smaller the further down it is examined, because fibres are all the way separating from it to end in the gray matter of the cord, where they join the mechanisms from which the motor fibres of the anterior spinal roots arise. The fibres of the pyramidal tract originate and have their nutritive centres in what is known as the motor area of the cerebral cortex: from there they converge and are collected into the ventral portion of the crus cerebri and pass through it and the pons Varolii to the ventral median portion (anterior pyramid) of the medulla oblongata, and there cross the

middle line at what is known as the *decussation of the pyr-amids* and enter the spinal cord on the opposite side. The area of descending degeneration, *dpt*, lying close to the anterior fissure is the *direct pyramidal tract.* Its fibres arise in the same cerebral region as those of pyramidal tract, and have a similar course and ending, except that they do not cross to the other side in the medulla oblongata, but gradually pass over in the spinal cord itself, to end in the gray matter connected with the origin of the anterior spinal roots: the direct pyramidal tract does not extend so far down the cord as the crossed tract, *pt.* Another tract of descending degeneration is *dc.al*, the descending antero-lateral: it represents rather an area over which are to be found some degenerated fibres scattered among many undegenerated, than a distinct group of fibres. The same may be said of *ct*, the *comma tract:* it only extends a short way down in the external posterior column of the cord after a hemisection has been made on the same side. Its fibres are posterior root-fibres running back in the white matter a little distance before entering the gray core.

A conspicuous tract of ascending degeneration is the *cere-bellar tract cb.t.* It lies on the outer side of the pyramidal tract and can be traced along the dorsal side of the medulla oblongata to the cerebellum. It commences in the lumbar region of the cord, and seems to contain two sets of fibres; some originating in the gray matter and passing on to re-enter it at a higher level of the cord; and others continued to the cerebellum. The nerve-fibres of this tract are very large. Another important ascending tract, *s, e, t, c*, lies in the median portion of the posterior white column and is named the *median posterior tract.* It commences in the lower portion of the cord and gradually increases in size upwards. Its degeneration follows not only section of the posterior column, but section of the dorsal roots of the spinal nerves: sections of these roots in the sacral, lumbar, thoracic, and cervical nerves cause degenerations in the areas marked respectively *s, e, t, c*; hemisection of the cord is followed above the section by degenerations in this tract corresponding to all the spinal nerves which join the cord below the section. The posterior median tract is lost as a distinct tract in the medulla oblongata: its fibres are nearly all small. The *ascending antero-lateral* tract, *ac.al*, contains many fibres which undergo degeneration after section of the cord on the same side, mixed with many fibres

which do not degenerate. It resembles the cerebellar tract and differs from the median posterior in only undergoing degeneration after section of the cord itself, and not of the posterior roots also. The upward ending of its fibres is still uncertain, but is probably in the cerebellum: the origin of the fibres is in the gray matter of the cord.

Allowing for all the tracts of degeneration above described it will be seen that considerable portions of the white columns of the cord (left unshaded in Fig. 175) are unaffected: at the most, trifling degenerations extending a little way above or below the point of cross-section are found. Some of these are due to bundles of posterior root-fibres which run for a short distance in the external posterior column, *epc*, before separating into two sets, one entering the gray matter of the posterior cornu, the other passing into the internal median tract. Another bundle of posterior root-fibres runs up in the cord a short way in what is named the *column of Lissauer*, *lt*, and gives rise to an ascending degeneration extending a short way above any hemisection. The main bulk of the unshaded parts of the figure, however, represents longitudinal fibres which do not degenerate up or down after section of the cord: they appear, therefore, to have nutritive centres at each end; and probably are fibres uniting different levels of the gray matter. In addition to the longitudinal are of course some horizontal: these are partly fibres of spinal roots passing into the gray core, partly medullated fibres crossing the middle line in the anterior white commissure; and in addition to fibres of the gray matter proper uniting its halves across the middle line are many fine medullated fibres which run dorso-ventrally and from side to side in it.

As regards longitudinal conduction in the white columns of the cord, we may sum up the main facts as follows: The pyramidal and direct pyramidal tracts consist of efferent fibres uniting the cerebral cortex with various levels of the gray matter of the cord from which motor fibres for the voluntary muscles pass out. The descending antero-lateral tract probably also contains efferent fibres uniting the brain with different parts of the gray matter of the cord. The cerebellar and ascending lateral tracts convey afferent impulses from the gray matter of the cord to the brain, but are only indirectly connected with the fibres of the dorsal spinal roots. The median posterior tract is afferent and mainly made of fibres

which pass directly from the dorsal spinal roots to the brain without intervention of the gray matter of the cord; but some of its fibres pass into the gray matter of the cord before reaching the medulla oblongata. Finally, the tracts which show no special ascending or descending degenerations are mainly made of longitudinal commissural fibres uniting different regions of the gray matter of the cord.

The Spinal Cord as a Reflex Centre. In order to explain physiological facts we must assume in addition to the special paths of union between parts of the gray matter of the cord afforded by certain fibres of the white columns, first, that a nervous impulse entering the gray network at any point may, under certain conditions, travel all through it, and give rise to efferent impulses emerging at any level; and, on the other hand, that there are certain lines or paths of easiest propagation between different points in this network, which the impulses keep to under ordinary conditions.

When a frog is decapitated it lies down squat on its belly instead of assuming the more erect position of the uninjured animal; its respiratory movements cease (their centre being removed with the medulla); the hind legs at first remain sprawled out in any position into which they may happen to fall, but after a time are drawn up into their usual position, with the hip and knee-joints flexed; having made this movement the animal, if protected from external stimuli, makes no other by its skeletal muscles; it has lost all spontaneity, and only stirs under the influence of immediate excitation. Nevertheless the heart goes on beating for hours; the muscles and nerves, when examined, are found to still have all their usual physiological properties; and, by suitable irritation, the animal can be made to execute a great variety of complex movements. But it is no longer a creature with a will, doing things which we cannot predict; it is an instrument which can be played upon, giving different responses to different stimuli (as different notes are produced when different keys of a piano are struck), and always the same reaction to the same stimulus; so that we can say beforehand what will happen when we touch it. Such actions are called *reflex* or *excito-motor* and fall into two groups: (1) *orderly or purpose-like reflexes,* which are correlated to the stimulus and are often defensive, tending, for instance, to remove an irritated part from the irritating object; (2) *disorderly or convulsive reflexes,*

not tending to produce any definite result, and affecting either a limited region or all the muscles of the body.

In higher animals similar phenomena may be observed. If a rabbit's spinal cord be divided at the bottom of the neck the animal is at first thrown into a flaccid limp condition like the frog, but it soon recovers. Voluntary movements in muscles supplied from the spinal cord behind the section are never seen again; but on pinching the hind foot it is forcibly withdrawn. Men, whose spinal cord has been divided by stabs or disease below the level of the fifth cervical spinal roots (above which the fibres of the phrenic nerve, which are necessary for breathing, pass out), sometimes live for a time, but can no longer move their legs by any effort of the will, nor do they feel touches, pinches, or hot things applied to them; if, however, the soles of the feet be tickled the legs are thrown into vigorous movement. As a rule, however, orderly reflexes are less marked and less numerous in the higher animals; in them the organization is less machine-like, the spinal cord being more the servant of the larger brain, and less capable of working without directions. Such animals, when intact, can to a greater extent control the muscular responses which shall be made to stimuli under various conditions; they have less automatic protection in the ordinary risks of life, but a greater range of possible protection. The human spinal cord, controlled by the brain, can adapt the reactions of the Body, with great nicety, to a vast variety of conditions; the frog's cord by itself does this for a smaller number of possible emergencies without troubling at all such brain as the animal has, but is less completely under the control of the higher centres for adaptation to other and more complex conditions. The difference being, however, but one of degree and not of kind, it is best to approach the study of the reflex actions of the human spinal cord through an examination of those exhibited by the frog.

The Ordinary Reflex Movements of a Decapitated Frog. For the occurrence of these the following parts must be intact: (*a*) the end organs of sensory nerve-fibres; (*b*) afferent fibres from these to the cord; (*c*) efferent fibres from the cord to the muscles; (*d*) the part of the spinal cord between the afferent and efferent fibres; (*e*) the muscles concerned in the movement. If the decapitated animal be suspended vertically after the shock of the operation is over, it makes a few attempts to hold its hind legs in their usual flexed position;

these soon cease, the legs hang down, and the creature comes
to rest. If one flank be now gently scratched with the point
of a pencil a reflex movement occurs, limited to the muscles
of that region; they twitch, somewhat as a horse's neck when
tickled by flies. If a pinch with small forceps be given
at the same spot, more muscles on the same side come
into play; a harder pinch causes also the hind leg of that
side to be raised to push away the offending object; more
violent and prolonged irritation causes all the muscles of
the body to contract, and the animal is convulsed. Here
then we see that a feeble stimulation causes a limited and
purpose-like response; stronger causes a wider radiation of
efferent impulses from the cord and the contraction of
more muscles, but still the movements are co-ordinated to
an end; while abnormally powerful stimulation of the sen-
sory nerves throws all the motor fibres arising from the
cord into activity, and calls forth inco-ordinate spasmodic
action. The orderly movements are very uniform for a given
stimulation; if the anal region be pinched, both hind legs are
raised to push away the forceps; if a tiny bit of bibulous paper
moistened with dilute vinegar be put on the thigh, the lower
part of that leg is raised to wipe it off; if on the middle of the
back near the head, both feet are wiped over the spot; if on
one flank, the leg and foot of that side are used, and so on;
in fact, by careful working, the frog's skin can be mapped
into many regions, the application of acidulated water to each
causing one particular movement, due to the co-ordinated
contractions of muscles in different combinations, and never,
under ordinary circumstances, any but that one movement.
The above purpose-like reflex movements may all be charac-
terized as defensive, but all orderly reflexes are not so. For
example, in the breeding season the male frog clasps the female
for several days with his fore limbs. If a male at this season
be decapitated and left to recover from the shock, it will be
found that gently rubbing his sternal region with the finger
causes him to clasp it vigorously.

Disorderly Reflexes or Reflex Convulsions. These come
on when an afferent nerve-trunk is stimulated instead of the
tactile end organs in the skin; or when the skin is very power-
fully excited; or, with feeble stimuli, in certain diseased states
(*pathological tetanus*), and under the influence of certain
poisons, especially strychnine. If a frog or a warm-blooded

animal be given a dose of the latter drug, a stimulus, such as normally would excite only limited orderly reflexes, will excite the whole cord, and lead to discharges along all the efferent fibres so that general convulsions result. It has been clearly proved that, in such cases, not the skin, or afferent or efferent nerves, or the muscles, but the spinal cord itself is affected by the poison (at least primarily), unless unnecessarily large doses have been given.

The Least-Resistance Hypothesis. In order to comprehend reflex acts we must assume a manifold union of afferent with efferent nerve-fibres; this is anatomically afforded by the minute plexus of the gray network, which is continuous through the whole cord, and in which many fibres of the anterior and posterior nerve-roots directly or indirectly end. The continuity of this network serves to explain general reflex convulsions, and the spread of an afferent impulse, or its results, through the whole cord, with the consequent emission of efferent impulses through many or all the anterior roots; but, on the other hand, it renders it difficult to understand limited and orderly reflexes, in which only a few efferent fibres are stimulated. To explain them we have to assume a great resistance to conduction in the gray network, so that a nerve impulse entering it is soon blocked and transmuted into some other form of energy; hence it only reaches efferent fibres originating near the point at which it enters, or fibres placed in specially easy communication with that. When the frog's flank is tickled, only muscles innervated from anterior roots on the same side of the body, and springing from the same level of the cord, are made to contract; when the stimulus is more powerful, the stronger afferent impulse radiates farther, but mainly in directions determined by lines of conductivity in the cord; *e.g.*, to the origin of the efferent fibres which cause lifting of the hind leg to the irritated spot. These paths of easiest conduction, or of least resistance, in some cases lie in the gray matter itself, in others in the *inter-central* or *commissural fibres* of the highly conductive medullated kind, which, passing out of the gray substance at one level, run in the white columns to it at another, where the efferent fibres of the muscles called into play originate. A still stronger afferent impulse radiates wider still, and, liberating energy from all the nerve-cells in the gray matter, produces a useless general convulsion. Under the influence of strychnine and

in pathological tetanus (as observed, for example, in hydrophobia), the conductivity of the whole gray matter is so increased that all paths through it are easy, and so a feeble afferent impulse spreads in all directions.

To account for the phenomena of localized skin sensations and of limited voluntary movements we must make a similar hypothesis. If the nervous impulses entering the gray network of the cord or, through fibres of the posterior median tract, the gray matter of the medulla oblongata, when the tip of a finger is touched spread all through it irregularly, we could not tell what region of the skin had been stimulated, for the central results of stimulating the most varied peripheral parts would be the same. From each region of the gray network where a sensory skin-nerve enters there must, therefore, be a special path of conduction to an anterior brain region, producing results which differ recognizably in consciousness from those following the stimulation of a different skin region. Possibly for true touch and temperature sensations these paths are in the post-median tract. The acuteness of the localizing power will largely depend on the definiteness of the path of least resistance in the gray matter, since while traveling in a medullated nerve-fibre from the skin to the cord, or (in the white columns) from the gray matter of the latter to the brain, the nervous impulse is confined to a definite track. Hence anything tending to let the afferent impulse radiate when it enters the gray network will diminish the accuracy with which its peripheral origin can be located. This we see in violent pains; a whitlow on the finger affects only a few nerve-fibres, but gives rise to so powerful nerve impulses that when they reach the cord they spread widely and, breaking out of the usual track of propagation to the brain, give rise to ill-localized feelings of pain often referred all the way up the arm to the elbow. Such cases are comparable to the transformation of an orderly reflex into a general convulsion when the stimulus increases.

As animals exhibit no, or at most limited, spontaneous movements when their whole cerebral hemispheres are removed, we conclude that the nerve impulses giving rise to such movements normally start in those parts of the brain. Thence they travel down the pyramidal tracts of the cord to its gray matter, which they enter at different levels, each in the neighborhood of a centre for producing a given movement. If they there radiated

far and wide no definite movement could result, for all the muscles supplied from the cord would be made to contract, and not merely those necessary to bend the index finger, for example. We must here again, therefore, assume a path of least resistance for the propagation of nerve impulses from a given fibre coming down from the brain, to the efferent fibres going to a certain muscle or group of muscles. The path between the two is almost certainly not direct; a co-ordinating spinal centre intervenes, and all that the brain has to do is to excite this centre, which then secures the proper muscular co-ordination. If the hand be laid flat on the table and its palm be rolled over, many muscles, including thousands of muscular fibres, have to contract in definite order and sequence. Persons who have not studied anatomy and who are quite ignorant of the muscles to be used can perform the movement perfectly; and even a skilled anatomist and physiologist, if he knew them all and their actions, could not by conscious effort combine them so well as the cord does without such direct interference. We have then to look on the cord as containing a host of co-ordinating centres for different muscles. These centres are put in nervous connection, on the one hand, with certain regions of the skin, and, on the other, with regions of the brain, and may be excited from either; in the former case the movement is called reflex; in the latter it may be reflex, or may be accompanied with a feeling of " will " and is then called voluntary. The more accurately the required centre, and no other, is excited, the more definite and precise the movement.

The Education of the Cord. Much of what is called educating our touch or our muscles is really education of the spinal cord. A person who begins to play the piano finds at first much difficulty in moving his fingers independently; the nervous impulses from the brain to the cord radiate from the spinal centres of the muscle which it is desired to move, to others. But with practice the independent movements become easy. So, too, the localizing power of the skin can be greatly increased by exercise as one observes in blind persons, who often can distinguish two stimuli on parts of the skin which are so near together as to give only one sensation to other people. Such phenomena depend on the fact that the more often a nervous impulse has traveled along a given road in the gray matter, the easier does its path become, and

the less does it tend to wander from it into others. We may compare the gray matter to a thicket; persons seeking to beat a road through from one point to another would keep the same general direction, determined by the larger obstacles in the way, but all would diverge more or less from the straight path on account of undergrowth, tree trunks, etc., and would meet with considerable difficulty in their progress. After some hundreds had passed, however, a tolerably beaten track would be marked out, along which travel was easy and all after-comers would take it. If instead of one entry and one exit we imagine thousands of each, and that the paths between certain have been often traveled, others less, and some hardly at all, we get a pretty good mental picture of what happens in the passage of nervous impulses through the gray matter of the cord; the clearing of the more trodden paths answering to the effects of use and practice. The human cord and that of the frog must not, however, be looked upon as pathless thickets at the commencement; each individual inherits cer-tain paths of least resistance determined by the structure of the cord, which is the transmitted material result of the life experiences of a long line of ancestors.

The Inhibition of Reflexes. Since it is possible, as by strychnine, to diminish the resistance in the gray matter, it is conceivably also possible to increase it, and diminish or prevent reflexes. Such is found to be actually the case. We can to a great extent control reflexes by the will; for example, the jerking of the muscles which tends to follow tickling: and it is found that after a frog's brain is removed it is much easier to get reflex actions out of the spinal cord. Certain drugs, as bromide of potassium, also diminish reflex excit-ability. If a frog's brain be removed and the animal's toe be dipped into very dilute acid, it will be removed after a few seconds; the time elapsing between the immersion and the lifting of the foot is known as the reflex time; anything diminishing reflex excitability increases this, as the stimulus (which has a cumulative effect on the centre) has to act longer before it arouses the cord to the discharging point. If the sciatic nerve of the other leg be stimulated while the toe is in the acid the reflex time is increased, or the reflex may fail entirely to appear. This is one case of a general law, that any powerful stimulation of one sensory nerve tends to in-hibit orderly reflexes due to the excitation of another. A

common example is the well-known trick of pinching the nose or upper lip to prevent a sneeeze. The whole question of reflex inhibition is at present very obscure. It may be due to the excitation of special fibres which inhibit reflex centres, as the fibres of the depressor nerve do the activity of the vaso-constrictor centre; or to the fact that one nerve impulse in the cord in some cases blocks or interferes with another; or partly to both.

Psychical Activities of the Cord. Since we can get quite marked reflex movements in the lower part of the Body of a man whose cord is divided and who cannot voluntarily move his lower limbs, and on questioning him find that he feels nothing and is quite ignorant of his movements unless he sees his legs, it is most probable that the spinal cord in all cases is devoid of centres of consciousness and volition: this is not certain, however; for there might well be a less division of physiological labor between the cord and brain of a frog, than between those of a man. Still we are entitled to good evidence before we admit that things so similar as the human cord and that of the frog possesses different properties. Co-ordinated movements following a given stimulus, or cries emitted by an animal, will not suffice to prove that it is conscious, since we know these may occur entirely unconsciously in men, who alone can tell us of their feelings. We must look for something that resembles actions only done by men consciously. In the frog it has been maintained that we have evidence of such. If a bit of acidulated paper be put on the thigh of a decapitated frog, the animal will bend its knee and use its leg to brush off the irritant; always using this same leg if the stimulus be not so strong as to produce disorderly reflexes. If now the foot be tied down so that the frog cannot raise it, after a few ineffectual efforts it will move the other leg, and may wipe the paper off with it. This it has been said shows a true psychical activity in the cord; a conscious and voluntary employment of new procedures under unusual circumstances. But a close observation of the phenomenon shows that it will hardly bear this interpretation; the movements of the other leg are very irregular and inco-ordinate, and much resemble reflex convulsions stirred up by the prolonged action of the acid, which goes on stimulating the skin nerves more and more powerfully. Even if new muscles came, in an orderly way, into play under the stronger

stimulus, that would not prove a volitional conscious use of them; we see quite similar phenomenon when there is nothing purpose-like in the movement. Many dogs reflexly kick violently the hind leg of the same side when one flank is tickled. If this leg be held and the tickling continued, very frequently the opposite hind leg will take on the movements, which it never does in ordinary circumstances. This is quite comparable to the frog's use of its other leg under the circumstances above described, but here it would be obviously absurd to talk of a volitional source for such a senseless movement.

Reflex Time. This is the time elapsing between the stimulation of a sensory surface and the resulting reflex contraction of a muscle. It contains, of course, several elements—the time taken in the origination and afferent course of the nerve impulse, the time occupied in the centre, and that in the efferent nerve-fibres, and the period of latent excitement of the muscles. Since the rate of travel of nerve impulses and the time of latent excitement are known with tolerable accuracy they can be estimated; and their sum subtracted from the whole time gives the time taken up in the central organ. This, as might be expected, when we consider the highly complex nature of the processes required to produce a co-ordinated reflex movement, is very much greater than the time occupied in traversing an equal length of nerve trunk. An electric shock given to one eyelid causes a reflex wink of both, and by suitable apparatus the time lapsing between stimulation of one eyelid and movement of the other can be measured. It is about .0660 sec.; the calculated time for the passage of the afferent impulse to the centre in the gray matter of the fourth ventricle and of the efferent to the orbicularis muscle of the other eyelid, or the period of latent excitation, is about .0160 sec., leaving .0500 sec. for the central processes. Reflex time varies considerably. It is longer for more complicated reflex movements; also the strength of the stimulus has an influence; if one toe of a decapitated frog be immersed in very dilute acid the time which elapses before it is withdrawn is greater than when the acid is a little stronger.

CHAPTER XXXVII.

THE PHYSIOLOGY OF THE BRAIN.

The Functions of the Brain in General. The brain, at least in man and the higher animals, is the seat of consciousness and intelligence; these disappear when its blood-supply is cut off, as in fainting; pressure on parts of it, as by a tumor or by an effusion of blood in apoplexy, has the same result; inflammation of it causes delirium; and when the cerebral hemispheres are unusually small idiotcy is observed. The brain has, however, many other important functions; it is the seat of many reflex, automatic, and co-ordinating centres, which can act as entirely apart from consciousness as those of the spinal cord. It is also traversed by many paths of conduction, some uniting it with the spinal cord and numerous others putting its own parts in anatomical connection.

The psychical activities, at least in man, seem to be dependent on the forebrain, the rest of the complex mass having other non-mental functions or at most being only concerned in very simple mental states. After the cerebral hemispheres have been removed from a frog it is still able to perform every movement as before, but it no longer performs any spontaneously. Suitably stimulated it will leap, swim, crawl, climb, turn off its back to its normal position; and if the optic thalami have not been injured will in leaping forward avoid an obstacle placed between it and the light. Its whole essential mechanism of movement is clearly intact, and can be thrown into action and to a certain extent be guided by afferent nervous impulses. Quite similar phenomena may be observed in pigeons; they not only can stand, but walk, fly if thrown into the air, and preen their feathers, after removal of the cerebral hemispheres; and if carefully tended will live for months. Mammals bear badly extensive operations on the forebrain and usually die before fully recovering from the shock of the operation; but rats survive some hours, and then exhibit very similar phenomena. However it has been

possible by repeated operations, taking away only a part at a time, to successfully remove almost all the surface gray matter of the cerebral hemispheres from dogs; and the animals have recovered so as to perform many ordinary movements so well that a person observing them only for a short time would notice nothing abnormal. But in such cases not only some cerebral cortex has been left but also the deeper lying corpora striata and optic thalami: when these gray masses and all the cerebral cortex are removed, as is possible in frogs and birds, the animal does not move unless directly stimulated, or so rarely that movements which appear due to a spontaneous volition are probably due to some unobserved irritation or stimulation. In addition to loss of willed movements there is loss or nearly complete loss of *perception*, that is, of the power of mentally interpreting and giving a meaning to incoming nervous impulses. The pigeon or rat will start at a loud noise, but makes no attempt to escape, as if it conceived danger; it will follow a light with the eyes but make no attempt to escape from a hand stretched out to seize it; it can and does swallow food placed in its mouth, but will starve if left alone with plenty of it, the sight of edible things seeming to arouse no idea or conception. It has been doubted whether the animals have any true sensations; they start at sounds, avoid opaque objects in their road, and cry when pinched; but all these may be unconscious reflex acts: on the whole it seems more probable, however, that they have sensations but not perceptions; they feel redness and blueness, hardness and softness, and so on; but sensations, as already pointed out, tell in themselves nothing; they are but signs which have to be mentally interpreted as indications of external objects or of conditions of the Body: it is this interpreting power which seems deficient in the animal deprived of its forebrain. In some cases a like state appears to occur in man in connection with abnormal states of parts of the cerebral hemispheres. The patient may have eye, retina, optic nerves and all the endings of these in the optic thalami and corpora quadrigemina intact, and his pupils react to light, and the eyes follow a bright object, yet the object arouses in the patient no idea as to its nature: apparently he sees it, but he is *mind blind.*

The Medulla Oblongata. Lying on the ventral aspect of this (Chap. XII) on the sides of the continuation of the anterior fissure of the cord are the two masses of nerve-fibres known

as the *anterior pyramids :* most of the fibres of these are continuations of the pyramidal tracts of the cord and here cross the middle line, forming thus the *decussation of the pyramids.* The fibres of the direct pyramidal tract pass on in the pyramid of the same side, only crossing in the cord. The pyramidal fibres pass on through the pons Varolii and along the ventral or basal side of the crura cerebri (Fig. 176), and enter the cerebral hemispheres. In the medulla are a number of masses of gray matter (often named nuclei) which have the same relation to the motor fibres of cranial nerves as areas of gray matter in the cord have to the motor fibres of the spinal roots, and from these motor nuclei medullated fibres join the pyramids and go with them into the forebrain. Such fibres of ascending degeneration in the cerebellar tract of the cord and of the ascending antero-lateral tract as extend above the cord run on the dorsal side of the medulla oblongata as the *restiform bodies ;* they diverge in front so as to lie on the sides of the fourth ventricle and enter the cerebellum. The fibres of the posterior median column terminate in a mass of gray matter in the medulla known as the *nucleus gracilis :* those of the exterior median column in a similar *nucleus cuneatus.* These nuclei in turn give origin to many fibres, a large number crossing the middle line, and some of these are then continued as the *fillet* along the dorsal side of the crus cerebri to the fore brain; others join the restiform body and through it the opposite side of the cerebellum: these crossings constitute the *sensory decussation,* as distinguished from the pyramidal or *motor.* The fibres of the antero-lateral descending tract which do not undergo descending degeneration probably join the pyramids; all their fibres entering the medulla from the cord end in gray matter of the medulla. By the word " ending " is meant, of course, only that they cannot be further traced as individual fibres, not that no physiological representatives of them arise in the gray matter of the medulla and pass to other parts of the brain.

The central canal of the spinal cord passes (Chap. XII) into the medulla oblongata, in the anterior portion of which it expands to form the fourth ventricle. The gray matter of the cord is continued around the canal and on the floor and sides of the ventricle; and in connection with it are special thickenings, rich in nerve-cells forming the *nuclei* or *deep origins* of most of the cranial nerves: some of these nerves arise from more

than one nucleus and some of the nuclei are separated from the gray matter around the central cavity, but a minute anatomical description would be here out of place. The *olivary capsules*, however, placed in the olivary bodies which lie on the outer side of each anterior pyramid may, however, be mentioned. The nerves having their nuclei in the medulla oblongata are the hypoglossal (xii), the spinal accessory (xi) except its spinal portion, the vagus (x), the glossopharyngeal (ix) (some fibres of which perhaps come from the cord), the auditory (viii) (by two distinct bundles of fibres, cochlear and vestibular, connected with distinct nuclei), the facial (vii), the patheticus (vi), part of the trigeminal. Some of the trigeminal arises from gray matter in the corpora quadrigemina. The nucleus of the abducens (iv) lies just under the floor of the aqueduct of Sylvius (Fig. 176), opposite the posterior border of the anterior corpora quadrigemina. The oculo-motor (iii) arises from gray matter under the front of the aqueduct and from the posterior part of the third ventricle. All the fibres of the above ten nerves arise, then, from gray matter around the cerebral continuation of the gray matter of the cord, and most of them behind the midbrain.

Besides its functions as affording paths between the cord and the rest of the brain and as the seat of many relay and junction centres the medulla has important reflex and automatic activities. As in the case of the cord, its motor centres may be thrown into reflex activity by afferent impulses from below, as well as by efferent travelling down from cerebrum or cerebellum. It is especially concerned with nervous control of the organs more immediately connected with circulation, respiration, and mastication. The physiological action of most of the medullary centres has already been described; the more important are—1. The respiratory centre. 2. The cardio-inhibitory centre; the centre of the accelerator heart-fibres lies in the medulla. 3. The vaso-motor centres. 4. The centre for the dilator muscle-fibres of the pupil. 5. The centre for the muscles of chewing and swallowing, which are commonly thrown into action reflexly, though they may be made to contract voluntarily. 6. The convulsive centre. 7. The diabetic centre. 8. The centre reflexly exciting activity in the salivary glands, when sensory nerves in the mouth are stimulated. 9. Certain centres for complex bodily movements; an animal with its medulla oblongata can execute

much more complicated reflex acts than one with its spinal cord alone.

The Cerebellum and Pons Varolii. (Figs. 74, 75). The anterior part of the medulla oblongata is covered above by the cerebellum and below by the pons, the latter of which is mainly a transverse commissure uniting the hemispheres of the cerebellum, though the pyramidal and other longitudinal commissural fibres run through it; and in it are many gray nuclei. The halves of the cerebellum are also united with one another by transverse fibres of its middle lobe; and, behind, by the *posterior peduncles* with the restiform bodies and the medulla, and, in front, by the *anterior peduncles*, with the cerebrum. Besides its gray surface with small nerve-cells and the cells of Purkinje (Fig. 82) it contains other more central gray matter. The most striking anatomical fact in relation to the cerebellum is its close connection with the afferent tracts of the spinal cord, nearly all of which except the fibres of the fillet are only connected with the cerebrum through the intervention of the cerebellum. The same is true of the vestibular portion of the auditory nerve and probably also of most of the afferent fibres of all the posterior cranial nerves. The cerebellum is thus subjected to influences from many regions of the Body; the skin, the muscles, the ears, and probably also the eyes are sources of impulses streaming into it all the time, and modifying the conditions of its gray matter and the nature of the impulses in turn issued from that. The most marked result of extensive injury of the cerebellum is muscular inco-ordination; it seems to be a chief organ of what we may call personally *acquired reflexes*, as distinguished from inherited.

Every one has to learn to stand, walk, run, and so on; at first all are difficult, but after a time become easy and are performed unconsciously. In standing or walking very many muscles are concerned, and if the mind had all the time to look directly after them we could do nothing else at the same time; we have forgotten how we learnt to walk, but in acquiring a new mode of progression in later years, as skating, we find that at first it needs all our attention, but when once learnt we have only to start the series of movements and they are almost unconsciously carried on for us. At first we had to learn to contract certain muscle groups when we got particular sensations, either tactile, from the soles, or muscular,

from the general position of the limbs, or visual, or others (equilibrium sensations, see below) from the semicircular canals. But the oftener a given group of sensations has been followed by a given muscular contraction the more close becomes the association of the two; the path of connection between the afferent and efferent fibres becomes easier the more it is travelled, and at last the afferent impulses arouse the proper movement without volitional interference at all, and while hardly exciting any consciousness; we can then walk or skate without thinking about it. The will, which had at first to excite the proper muscular nerve-centres in accordance with the felt directing sensations, now has no more trouble in the matter; the afferent impulses stimulate the proper motor centres in an unconscious and unheeded way. Injury or disease of the cerebellum produces great disturbances of locomotion and insecurity in maintaining various postures. After a time the animals (birds, which bear the operation best) can walk again, and fly, but they soon become fatigued, probably because the movements require close mental attention and direction all the time.

Sensations of Equilibrium. In order to make proper movements of balancing or locomotion we need a knowledge of the space relations of the Body to its surroundings. When eyes, muscles, and skin send in concordant afferent impulses, movements are precise; if sensations of any one of these groups are wanting (excluding blind persons who have learned to do without some of them) or abnormal the whole mechanism is thrown out of gear. Persons who have lost muscular or tactile sensibility stand and walk with difficulty; those who have *nystagmus* (jerking unconscious movements of the eyeballs which cause the visual field to seem to move in space) do the same and feel giddy; and, if a person be rapidly rotated with his eyes open he soon becomes giddy; the succession of retinal images suggests that he is moving in space, but the muscular and tactile afferent impulses are in conflict with that; and though this discordance hardly comes into direct consciousness as a definite contradiction between sensations, the want of harmony in the afferent impulses throws co-ordinating motor mechanisms out of gear, with resulting uncertainty in locomotion. An important group of afferent impulses concerned with the maintenance of bodily equilibrium in addition to those above referred to is probably derived through the semi-

circular canals of the ear, which are supplied by the vestibular portion of the auditory nerve; and it has, as we have seen, a special cerebellar connection. An old view was that, lying in three planes at right angles to one another, they served to distinguish the direction of sound-waves reaching the ear; but as the direction of oscillation of the tympanic ossicles is the same, no matter what that of the sound-waves entering the external auditory meatus may be, such an hypothesis has no foundation. The cochlea sufficiently accounts for the appreciation of notes, and such noises as are due to inharmonically combined tones; while the sacculus will suffice for other noises: and it is found that disease of the semicircular canals does not interfere with hearing, but often causes uncertainty of movements and feelings of giddiness.

Experiment shows that cutting a semicircular canal is followed by violent movements of the head in the plane of the canal divided; the animal staggers, also, if made to walk; and, if a pigeon and thrown into the air, cannot fly. All its muscles can contract as before, but they are no longer so coordinated as to enable the animal to maintain or regain a position of equilibrium. It is like a creature suffering from giddiness; and similar phenomena follow, in man, electrical stimulation of the regions of the skull in which the semicircular canals lie.

If, moreover, a person lie perfectly quiet with closed eyes on a table which can be rotated, he is able to tell when the table is turned and in which direction, and often with considerable accuracy through what angle. If the rotation be continued for a time the feeling of it is lost, and then when the movement ceases there is a sense of rotation in the opposite direction. In such case neither tactile, muscular, nor visual sensations can help, and in the semicircular canals we seem to have a mechanism through which rotation of the head could give origin to afferent impulses, whether the head be passively moved with the rest of the Body or independently by its own muscles. Movements of endolymph in relation to the walls of the canals may act as stimuli by causing a swaying of the projecting hairs of the ampullæ (Fig. 167). Place a few small bits of cork in a tumbler of water, and rotate the tumbler; at first the water does not move with it; then it begins to go in the same direction, but more slowly; and, finally, moves at the same angular velocity as the tumbler.

Then stop the tumbler, and the water will go on rotating for some time. Now if the head be turned or rotated in a horizontal plane similar phenomena will occur in the endolymph of the horizontal canal; if it be bent sidewise in the vertical plane, in the anterior vertical canal; and if nodded, in the posterior vertical; the hairs moving with the canal would meet the more stationary water and be pushed and so, possibly, excite the nerves at the deep ends of the cells which bear them, and generate afferent impulses which will cause the general nerve-centres of bodily equilibration to be differently acted upon in each case. Under ordinary circumstances the results of these impulses do not become prominent in consciousness as definite sensations; but they are probably always present. If one spins round for a time, the endolymph takes up the movement of the canals, as the water in the tumbler does that of the glass; on stopping, the liquid still goes on moving and stimulates the hairs which are now stationary; and we feel giddy, from the ears telling us we are rotating and the eyes that we are not; hence difficulty in standing erect or walking straight. A common trick illustrates this very well: make a person place his forehead on the handle of an umbrella, the other end of which is on the floor, and then walk three or four times round it, rise, and try to go out of a door; he will nearly always fail, being unable to combine his muscles properly on account of the conflicting afferent impulses. This and the feeling of rotation in the contrary direction when a previous rotation ceases become readily intelligible if we suppose feelings to be excited by relative movements of the endolymph and the canals inclosing it.

The Midbrain. The general arrangement of these parts has been already described (Fig. 82). Cross-sections show (Fig. 176) the aqueduct of Sylvius, *S*, traversing the midbrain near its upper part and surrounded by a thin layer of gray matter, in close connection with which are the origins of the third and fourth cranial nerves, IV, and of part of the fifth. The crura cerebri form the main mass of the midbrain. Each is divided by gray matter (*locus niger*, *Ln*) into a ventral portion (*pes* or *crusta*, *P*), which forms the semicylindrical portion of the crus seen on the base of the brain and a dorsal portion, the *tegmentum*, *Tg*. The pes consists mainly of the fibres of the pyramidal tract, *Py*, but some fibres of the fillet, *f*, also run forward in it, as do fibres, *fr* and *oc*, connecting

it with the frontal and occipital lobes of the cerebral hemisphere. The tegmentum contains gray masses and many transverse and longitudinal fibres. Many of the fibres, *cp*, come from the anterior peduncle of the cerebellum; these cross in the posterior part of the tegmentum; most of them end in a large mass of gray matter in the front of the tegmentum named the *red nucleus*; others run forward to the optic thalamus direct. Other longitudinal fibres are continued from the fillet some of

FIG. 176.—Diagram of cross-section of midbrain in region of posterior corpora quadrigemina : *P*, pes; *Ln*, locus niger; *Tg*, tegmentum, *S*, aqueduct of Sylvius; *cq*, right corpus quadrigeminum. In the pes on left side are indicated by *fr*, fibres from frontal lobe of cerebral hemisphere; *f*, fibres of fillet; *py*, fibres of pyramidal tract; *oc*, fibres from occipital lobe of cerebral hemisphere. In tegmental region, *f'*, fillet fibres to anterior corpus quadrigeminum; *f''*, fillet fibres for posterior corpus quadrigeminum; *cp*, fibres from cerebellar peduncle. Parts containing gray nerve matter are shaded in horizontal lines.

these, *f''*, end in the posterior corpora quadrigemina; others, *f'*, in the superior corpora quadrigemina and the occipital region of the cerebral hemispheres. The corpora quadrigemina are covered by a layer of medullated fibres, but their main mass is gray matter. The anterior pair are closely connected with the optic tracts, and therefore with the optic nerves and the retinas: to their outer sides and in front are the external *corpora geniculata*, gray masses closely associated with the optic tracts.

The structure of the midbrain shows that it is in great part merely a commissure between the parts in front of and behind it: but its connection with fibres of the optic tract shows that it has a close relation to visual sensations; and the origin in it of the oculo-motor and abducens nerves, that from it the eye muscles, and the iris and ciliary muscle are innervated.

The Brain Regions in Front of the Midbrain. It would be quite a hopeless task to attempt in a few pages any detailed account of the topography of these, but in addition to the facts already stated a few points of special physiological significance may be indicated. These portions of the brain may be in general described as consisting of three masses of gray matter on each side; optic thalamus, corpus striatum, cerebral

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FIG. 177.—Diagram to illustrate cerebral distribution of fibres proceeding from the pes of the crus cerebri. For description see text.

cortex. They are united in manifold ways by the transverse, longitudinal, and oblique fibres of the white substance of the cerebral hemisphere. Their more fundamental relations to the midbrain and to one another are shown in a very simplified and diagrammatic manner in Figs. 177 and 178. The *iter*, or aqueduct of Sylvius, *i*, is seen passing into the posterior end of the third ventricle, 3, which is separated by only a very thin layer of white matter from the large ovoid gray mass *ot*, which is the optic thalamus. Connected by the

foramen of Monro, *fM*, with the third ventricle is the left lateral ventricle, *2,* bounded on the inner side by the thin septum lucidum. Between the septa lucida is the fifth ventricle, *5.* The gray mass, *Nc*, to the side of the lateral ventricle is the *caudate nucleus* and the mass *Ln* the *lenticular nucleus* of the corpus striatum. In front and at a level diferent from that of the diagram the two are continuous.

The band of white fibres, *ic*, lying here between the lenticular nucleus on the outer side and the caudate nucleus and optic thalamus on the inner side is the *internal capsule:* *ec* is the *external capsule.* *Fl* is the cortical gray matter of the frontal lobe of the cerebrum; *Pl*, of the parietal lobe; *Oc.l.* of the occipital lobe: *Ro*, the fissure of Rolando; *Po*, the parieto-occipital fissure. The course of many fibres in the forebrain is still uncertain, but some important paths have been traced by anatomical and microscopic work, and still more by following tracts of degeneration resulting from certain lesions, as in the case of the spinal cord; and also by noticing the results of stimulation or removal of definite areas.

Taking first the pes of the crus cerebri (Fig. 176), which consists entirely of longitudinal fibres, we find that the pyramidal tract, *py*, Fig. 177, is continued through the internal capsule and radiates beyond it, to end in the cortex of the frontal and parietal lobes in the region of the fissure of Rolando. These fibres are all efferent and degenerate to their endings in the gray matter of the cord or the motor nuclei of cranial nerves when the cortex in the Rolandic region is removed. A second collection of fibres in the pes is the frontal, and its fibres, *fr*, can be traced to the frontal region of the cortex; when that is removed the fibres degenerate as far as the gray matter of the pons, from which they are probably connected by other fibres with the opposite side of the cerebellum. A third set of fibres in the pes is the temporo-occipital, *oc*: they also pass through the internal capsule to the corresponding region of the cortex: they can be traced as far as the gray matter of the pons, and appear to be fibres of descending degeneration. Another set of fibres, *ca*, of descending degeneration in the internal capsule has no immediate connection with the cortex: it arises in the caudate nucleus; the course of the fibres beyond the pons is not known. The lenticular nucleus also gives off fibres, *g*, to the internal capsule, which probably connect the corpus striatum through the pes with the pons and

medulla oblongata, but they are so mingled with other fibres that they have not been satisfactorily traced.

Passing now to the tegmentum, it is first to be borne in mind that many fibres (including most of those of the anterior cerebellar peduncle) entering it from behind, end in the large *red nucleus* lying in its anterior portion and in its other gray masses. From these (Fig. 178) numerous fibres, *rn*, pass to the optic thalamus: so that the majority of the tegmental fibres differ from the pedal in that they only have indirect connection with the cortex through the thalamal and other gray matter. The thalamus is united with nearly all regions of the cortex by fibres, *af*, passing from its outer side into the internal capsule, and distributed in special abundance to the occipital lobe. Since the thalamus receives fibres through the tegmentum from the anterior quadrigemina and the lateral geniculata (which we have seen to have close connection with the optic nerves), and there is independent reason for believing parts of the occipital lobe to be closely associated with visual perceptions, the close anatomical association of that lobe with the thalamus is significant. Another group of fibres, *d*, connects the thalamus with the temporal and occipital cortex, but does not take its path through the internal capsule. Some fibres of the tegmentum reach the cortex without primary connection with the thalamus: of these is a set, *e*, which passes through the lenticular nucleus (but without any communication with its gray substance) on its way to the frontal and parietal lobes. At *ce* is indicated a set of fibres of the tegmentum which there is some reason to believe run to the fore part of the cortex direct, having no connection with the thalamus and passing ventral to the internal capsule.

Most of the fibres of the fillet, we have seen, end in the red nucleus or corpora quadrigemina: fibres arising in these gray masses connect them with the thalamus and through it with the cortex.

Besides fibres connecting the cortex with other parts are many which unite different cortical areas directly. A vast number (*Ca*, Fig. 177) cross the middle line in the corpus callosum and are believed to join corresponding parts of the two hemispheres. Others pass over in the small white anterior commissure and unite the two olfactory lobes and portions of the temporal lobes. The posterior commissure unites mainly the optic thalami and the front ends of the

tegmenta. The soft commissure is mainly gray matter. Finally a large number of associational fibres, *as*, unite different parts of the cortical substance of the same hemisphere.

The different gray masses on the same side of the forebrain are also united by fibres. They are either so scattered among others that they cannot be tracked out along special tracts of degeneration; or, as is possible, resemble some of the com-

1

Fig 178.—Diagram to illustrate cerebral distribution of the fibres proceeding from the tegmentum. For description see text.

missural fibres uniting upper and lower regions of gray matter in the spinal cord in having nutritive centres at each end, and therefore not degenerating on either side of a section. In any case very little is known as to their numbers or paths: their existence is indicated by the dotted lines in Figs. 177, 178.

Omitting the associational and the cross commissure fibres and those uniting the corpora striata and optic thalami,

it may be said in general that the systems of fibres represented in Fig. 177 are all almost certainly concerned in conveying impulses from the cortex, and those in Fig. 178 in the transmission of afferent impulses. It will be noted that both afferent and efferent fibres are abundant in the internal capsule; and that the corpus striatum and pes are more especially connected with efferent and the tegmentum and thalamus with afferent impulses. It can hardly be necessary to add that each line in the diagrams represents hundreds of thousands of nerve-fibres.

The Functions of the Cerebral Cortex. That this part of the nervous system is in close association with the intellect and with the initiation of voluntary movements seems beyond doubt: but it may have other functions quite apart from any states of consciousness; and intelligence and every volition may not entirely depend on it. The experiments made in recent years on the lower animals tend to the conclusion that some will and some intellect may remain in animals all or almost all of whose gray cerebral surfaces have been removed; the more complete loss of those powers described by earlier workers being due to the fact that the animals were not kept alive long enough after the operation. It has been observed that a dog whose cerebral cortex (as verified by subsequent post-mortem examination) had been nearly completely removed did learn after some months to walk about to all appearance voluntarily, and to find and eat his food; he even learned not to take the food of other dogs after he had been severely bitten several times for so doing. But more complex perceptions were lost: before the operation, for example, he was greatly terrified by seeing a man fantastically dressed, but afterwards no such appearance aroused in him so complex a conception as that of a strange or dangerous object. He also never recovered the trick of " giving paw," which had previously been taught him. But on the whole a person casually observing him would not have thought him very different from any other dog, except perhaps that he was rather stupid: put into a low open box, for example, he would not jump out of it when called, though he easily could do so and clearly desired to. Such simple and fundamental perceptions and volitions as remained in this and some similar cases probably have their seats in the optic thalami and corpora striata, and indeed embryology shows that the corpora striatum is morphologically a part of the

cerebral cortex: it is therefore probable that in man some of the lower and simpler mental faculties are associated also with those parts. There are, however, great and obvious chances of error in arguing from the actions of the lower animals as to their mental state: and these are increased by the comparatively small proportion the cerebral cortex bears to the whole cerebro-spinal centre in these animals when compared with its ratio in man, showing its less importance in the management of their actions. Hence the most useful observations are those made of late years on apes and monkeys and on men suffering from local brain disease. By utilizing these it has been possible to map out certain areas of the brain surface as having special, though possibly not absolutely unshared association, with volitional movement and with groups of sensations and sensory interpretations. In addition to facts obtained by removal or local disease of parts of the brain we have others obtained by electrical stimulation of certain parts of the cortex, which although quite insensible to cutting or mechanical irritation does in some places respond to application of the interrupted or constant electric current. The more important results obtained are indicated in a general way in Figs. 179 and 180, representing respectively the outer and inner surfaces of the right cerebral hemisphere; these diagrams should be compared with the more detailed figures in Chapter XI.

The shaded area beginning on the top of the brain and extending down the sides of the fissure of Rolando or central fissure, *Ro,* and beyond its ventral end is the motor area of the cortex. It also extends to the inner side of the hemisphere, as shown in Fig. 179. Electric stimulation of different parts of this area causes movements of leg, arm, or face as indicated. Removal of the region marked " arm " in the monkey causes motor paralysis and some loss of sensibility in the arm on the opposite side of the body. It is also followed by degenerations extending from the removed region of cortex through the internal capsule to some pyramidal fibres in the pes and thence back through the pyramids to the crossed pyramidal and direct pyramidal tracts in the cord as far as the cervical enlargement. Localized disease of this area in man is followed by paralysis of voluntary movements of the opposite arm and by similar degenerations. Similar statements are true

for the areas marked leg, foot, and face, except that the resulting degeneration would extend in the one case to the lumbar enlargement of the cord, in the other to the nucleus of the VII nerve in the medulla. Moreover, each of these areas can be mapped out into smaller ones, giving origin to a more limited movement when stimulated and a more limited paralysis and tract of degeneration when removed. Thus areas especially associated with the eyelids, with the muscles of the angle of the mouth, with the flexor muscles of
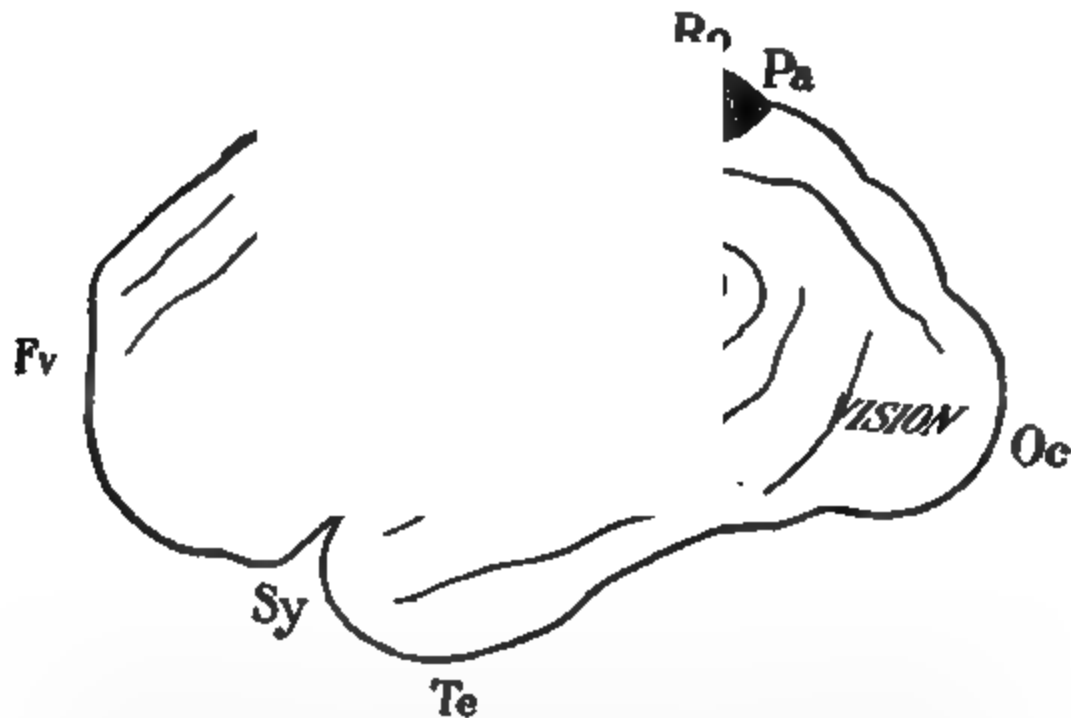
Fig. 179.—Diagram of outer surface of left cerebral hemisphere to illustrate the localisation of functions. The motor area is shaded in vertical and transverse lines: *Sy*, fissure of Sylvius; *an*, angular gyrus or convolution; *Ro*, fissure of Rolando; *Fv*, frontal lobe; *Pa*, parietal lobe; *Te*, temporal lobe. Only a very few of the more important fissures are indicated. Compare with Fig. 180.

the wrist, all have their definite places in the general face or arm region. So definite are the positions of these areas that in cases of localized paralysis, diagnosed as due to lesions of the cerebral cortex, surgeons now have no hesitation in opening the skull in order if possible to remove the cause of trouble, as a small tumor: they know precisely in what spot they will find it. Although the localization is therefore tolerably precise, yet the limits of neighboring areas are not as sharp cut as the boundaries of neighboring countries on a map: as shown in Fig. 179, the arm area in its lower part overlaps part of the face area; and the minor areas within the main ones also overlap one another at their margins.

The general interpretation put upon the above facts, and one which seems justified, is that in making definitely *willed*

movements the cortical area connected through the pyramidal tract with the muscles concerned is the place from which efferent impulses start throwing into action lower centres which more immediately co-ordinate the muscles: these lower centres in midbrain, cerebellum, medulla or cord may of course be thrown into reflex action by afferent impulses having no connection with the cortex, and to the eye the resulting movement would be exactly the same as a willed one. In another person, and still more in a dog or monkey, we must often be in doubt whether an action is or is not intentional; and as already pointed out, many movements of our own which were at one time even painfully intentional become quite unconscious after practice and are carried out by lower centres. It is also to be borne in mind that the cortical area from which the efferent processes of a willed movement make their start is in connection by associational and other commissural fibres with many other regions of the cortex, and with fibres from the optic thalamus which may bring nerve impulses exciting it, and it is also in connection with the whole gray cortical network, so that the brain antecedents or excitants leading to a given movement, either alone or in combination with others, may be very different, and may be associated or not with concomitant sensations or emotions.

Take such a movement as clenching the fist. On a corpse this might be brought about by pulling on the flexor tendons of the digits, but in an imperfect way; or, again in a very imperfect manner by stimulation of the motor nerves of the flexor muscles in the arm of a living person. If, however, we knew exactly the proper sensory fibres in spinal nerve-roots to stimulate and could thus act on the centre co-ordinating the proper muscles, there is no doubt we could bring about reflexly, and apart from all consciousness, a quite normal clenching movement. Next suppose a person struggling for breath: as his extraordinary muscles of respiration come into play his fists are clenched; here impulses from the medulla oblongata travel down the cord and throw the " clenching " spinal centre into activity along with many other muscles, and co-ordinating them all so as to give as good a pull as possible to all muscles which can help an inspiration. In a higher but still not volitional stage, more groups of muscles are concerned, and centres of co-ordination in the pons and

cerebellum come into action also; take a man preparing for a high jump: as he crouches and puts himself in balance for the spring he clenches his fists, quite unconsciously of course. Here the immediate clenching centre is thrown into activity along with the muscles of breathing, and of all parts of the trunk and limbs. Each subsidiary peripheral centre plays its part and the instreaming afferent impulses from the skin of the feet, from the fibres of the muscular sense, from the semicircular canals, from the eyes, are all concerned (without the person's perception of them) in throwing the motor mechanisms of midbrain, cerebellum, medulla, and cord into harmonious activity, so that when the jump is actually willed it shall be accomplished. But that in this case the volition plays a very secondary part is obvious; it merely acts on an apparatus all ready to discharge in a given way when a suitable additional nerve impulse reaches it. A runner all tense for the start of a hundred-yard race can hardly be said to start voluntarily when he hears the signal; the case is comparable more to the self-balancing of a pigeon deprived of its cerebral hemispheres, when its perch is tilted. Next, suppose I clench my fist "involuntarily," as we commonly say, when I see something that arouses my indignation; here clearly a mental element is in play, but not a volitional one, and so far as the movement is concerned probably the motor area of the cortex has little or nothing to do with it: it is more in accord with what is seen on animals to suppose that such simple emotions and their characteristic movements may be carried out by nerve apparatuses lying no higher than the thalami and corpora striata. If, however, I strike a man with the intention to punish him, there can be little doubt that the "clenching" centre is excited by fibres from the cortex and passing down in the pyramidal tract. But this cortical area may in turn be thrown into activity and may have its tendency to discharge modified in many ways. My anger may be the culminating result of many long past received and interpreted and remembered sensations, and whether I shall give the blow or restrain myself also be dependent on many antecedents of experience. Again, I clench my hand to knock down a madman, as the only immediate method of preventing him from committing a murder: here the same motor cortical area no doubt would be thrown in action as when the blow was struck in anger, but it is clear that the

antecedent nerve processes arousing its activity would be quite different in the two cases; and they would yet again be different if I clenched the fist in order to explain to a child the meaning of the word *clench*. We see then that the immediate motor centres may be excited in various ways and in various combinations quite apart from the cortex of the cerebrum and by fibres not connected with the pyramidal tracts; and that when excited from the cortical area of the cerebrum through fibres of the pyramidal tract, that area itself may be excited or controlled in its activity by a vast number of other parts of the cortex, and by non-cortical parts of the nervous system. The motor area cannot properly be spoken of as the seat of volition: an act of willing is the final outcome of changes in other and often numerous other regions of the cortex, the resultant of whose material processes is a discharge of efferent impulses from some region of the motor area.

The permanent effects of local lesions of the Rolandic region differ with the development of the brain. In dogs removal of the left brain region connected with the fore paw causes only temporary motor paralysis of the limb on the other side; after a time the animal learns to walk again as well as before; then removal of the corresponding area on the right side of the brain is followed by paralysis of both fore limbs. This has been supposed to show that the centre on the right side had taken up the duty of control for both sides after that on the left had been removed. However that may be, the second paralysis is also only temporary, disappearing in some weeks or months; and as has been already stated, even after removal of all the motor area the animal occasionally learns in the course of time to walk nearly as well as ever. This must be due to lower centres (corpora striata ?), and the question is whether the movements in such cases are truly volitional, for definite acts of willing a movement probably play a very small part in a dog's life: most of its movements are the immediate efferent expression of afferent impulses and true volitions have but a small part in them. In the lower monkeys definite motor effects of removal of part of the cortical motor area are also temporary, but last longer than in dogs; and in the anthropoid apes the same is the case in a greater degree, and according to some experimenters certain delicate combined movements are permanently lost

after destruction of the motor area. These facts are correlated with the relatively larger size of the cortical motor area and of the pyramidal tracts in monkeys as compared with dogs, and the anthropoid apes as compared with other monkeys. The larger and more highly organized the brain area the greater the part it plays in the life-work of the animal and more noticeable are the results of its absence. In man local paralysis due to local cortical lesion is often only temporary: this may be due to disappearance of the disease; or to the primary paralysis being only a " shock " effect, and not due to actual disease of the motor centre, for it is well known that in animals injury to one region of the brain will often for a considerable time inhibit the activity of other parts: or it may be due to the hemisphere of the opposite side assuming control. Different observers attribute very various values to these three possible factors. In this connection reference may be made to cases of what is called *aphasia*, which in its fully developed state is a loss of the power to apply words to express ideas. The power of speech may, of course, be lost through disease of the larynx or paralysis of the nerves or muscles of the voice organs, but such a condition is not true aphasia: the aphasic person can often articulate perfectly well, but he cannot attach a meaning to his spoken word: in some cases he can write words with meaning, though he cannot say them; in other cases (*agraphia*) the power of using written words to express ideas is also lost, though the person can write, and his general conduct shows that he is still guided by his intelligence; he knows quite well what he wants to say, but he cannot set the proper motor apparatus in action to utter the word: if he speaks, the word has no connection with that in his mind, and as soon as he hears himself speaking it he often knows that the word he uses is quite wrong. We find in such cases the power to understand words, and to form ideas of words, and to utter words, but some link between the origin of the idea and the discharge of the motor impulses willed to express it is out of gear. It is as if an injured reflex centre should give a wrong or inco-ordinate efferent response to an afferent impulse. Aphasia is almost invariably connected with disease of the area marked *SP* in Fig. 179 and known as the third or lower frontal convolution, and the pathological change is on the left side of the brain only. The area, as will be seen, is closely associated with the face area and the tongue

and partly overlaps them, or rather is intermixed with them; as pointed out above, the lesion is not one of motor speech centres, but of the connection between these and other cerebral areas in which have occurred changes accompanied by the desire of verbal expression; something wrong probably in the gray network. Very rarely aphasia has been known to follow disease or injury of the corresponding convolution on the right side; so that in it we have an example of a very definite nexus between a limited area of the cortex and the expression of will through movements. Cases of recovery from aphasia have occurred, but are extremely rare. In the exceptional cases it has been supposed that the right side of the brain takes up the duty of connecting the material changes in the gray network which accompany the origination of an idea in one or more cortical areas, with the other changes which result in speech. This view gains some support from the fact that in certain cases of recovery due to left-side disease, subsequent disease in the third right frontal convolution has been followed by a fresh aphasia. But however that may be we have in aphasic persons definite evidence of the limitation of definite function to a very limited area or areas of the cerebral cortex.

Much less is known as to other regions of the cortex than of the motor area: most of them do not respond to electrical stimulation at all, and those areas that do, only show it by movements lacking in precision. We are reduced, therefore, to observation on animals from whom certain cortical parts have been removed, and to observations on diseased persons. Certain broad regions have in this way been mapped out as connected with certain main groups of sensations (Figs. 179, 180), probably rather with the combining and interpreting of sensations, with their *ideation*, than with the mere raw sensation itself. The latter is probably more dependent on the lower brain centres; in most cases it is secondary changes in these which lead to impulses which are passed on to excite the cortical sensory areas.

There is considerable evidence that removal or extensive injury of the left occipital lobe causes blindness of the left half of each retina, and *vice versa*. Also, that stimulation of this region of the brain may cause movements of the eyes and eyelids which have been described as such as an animal would make if it thought it saw something, though obviously

that must be a very uncertain deduction. Also, the optic tract of each side has through the anterior corpus quadrigeminum and some other gray masses a close connection with the cortex of the occipital lobe. Probably, therefore, that region has some close connection with vision. There is also some evidence that the *angular gyrus* (*an*, Fig. 179) has connection with sight.

The sense of smell has been supposed especially connected with the uncinate gyrus of median side of the temporal lobe (*un*, Fig. 180), and the sense of taste with a neighboring
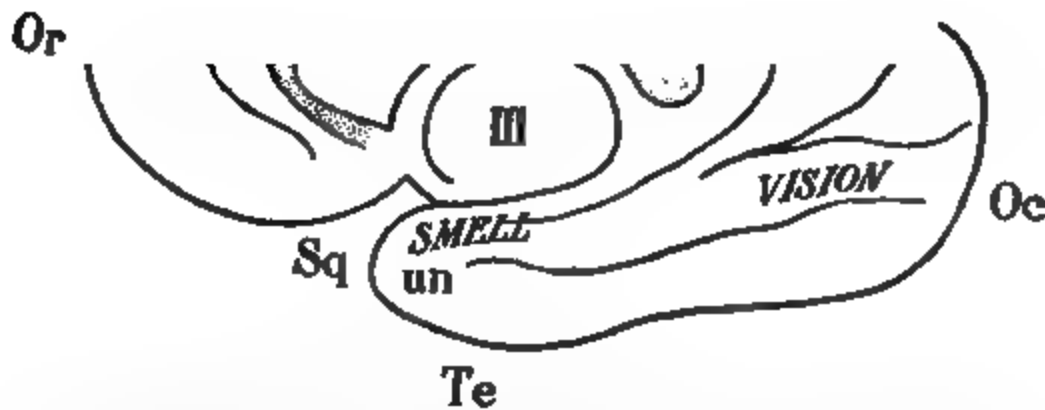
Fio. 180.—Diagram of inner surface of left cerebral hemisphere to illustrate cerebral localization. *Sq,* fissure of Sylvius; *Ro,* fissure of Rolando; *Fr,* frontal lobe; *Oc,* occipital lobe; *Te,* temporal lobe; *C.cl,* corpus callosum; *III,* third ventricle. Compare with Fig. 179.

area, but the evidence is unsatisfactory; and the same may be said of the reasons which led to designation of the region of the temporal lobe close behind the fissure of Sylvius with hearing. The region marked on the diagram as that of cutaneous sensations has also a doubtful claim : there is some reason to believe that the motor area of the cortex has connection with the muscular sense; also to some extent with tactile feelings.

Tactile and temperature impulses cross the middle line somewhere on their path from the skin to the brain. An apoplectic effusion in one cerebral hemisphere causes loss of sensation and of voluntary movement on the other side of the Body.

The frontal lobes are quite irresponsive to excitation, and considerable parts of them have been removed without ap-

parent diminution of motor or sensory faculty. By a sort of process of exclusion, the rest of the cortex being allotted (though on unsatisfactory evidence) to motion and sensation the frontal regions have been supposed to have special connection with the higher intellectual faculties.

Mental Habits. Movements which are commonly executed together tend to become so associated that it is difficult to perform one alone; many persons, *e.g.*, cannot close one eye and keep the other open. From frequent use, the paths of conduction between the co-ordinating centres for both groups of muscles have become so easy that a volitional impulse reaching one centre spreads to the other and excites both. This association of movements, dependent on the modification of brain structure by use, finds an interesting parallel in the psychological phenomenon known as *the association of ideas;* and all education is largely based on the fact that the more often brain regions have acted together the more readily, until finally almost indissolubly, do they so act. If we always train up the child to associate feelings of disgust with wrong actions and of approbation with right, when he is old he will find it very hard to do otherwise: such an organic nexus will have been established that the activity of the one set of centres will lead to an excitation of that which habit has always associated with it. The higher nerve-centres are throughout eminently plastic; it is that which marks them out for a far higher utility and greater adaptation to the varying experiences of individual life than the more fixed and machine-like lower centres: every thought leaves in them its trace for good or ill; and the moral truism that the more often we yield to temptation—the more often an evil solicitation, sensory or otherwise, has resulted in a wrong act—the harder it is to resist the repetition of it, has its parallel (and we can hardly doubt its physical antecedent) in the marking out of a path of easier conduction from perceptive to volitional centres in the brain. The knowledge that every weak yielding degrades our brain structure and leaves its trail in that organ through which man is the " paragon of animals," while every resistance makes less close the bond between the thought and the act for all future time, ought surely to " give us pause: " on the other hand, every right action helps to establish a " path of least resistance," and makes its subsequent performance easier.

The brain, like the muscles, is improved and strengthened by exercise and injured by overwork or idleness; and just as a man may specially develop one set of muscles and neglect the rest until they degenerate, so he may do with his brain; developing one set of intellectual faculties and leaving the rest to lie fallow until, at last, he almost loses the power of using them at all. The fierceness of the battle of life nowadays especially tends to produce such lopsided mental developments; how often does one meet the business man, so absorbed in money-getting that he has lost all power of appreciating any but the lower sensual pleasures; the intellectual joys of art, science, and literature have no charm for him; he is a mere money-making machine. One, also, not unfrequently meets the scientific man with no appreciation of art or literature; and literary men utterly incapable of sympathy with science. A good collegiate education in early life, on a broad basis of mathematics, languages, and the natural sciences, is a great security against such imperfect mental growth; one danger in American life is the tendency to put lads in a technical college, or to start them in business before they have attained any broad general education. Another danger, no doubt, is the opposite one of making the training too broad; a man who knows one or two literatures fairly well, and who has mastered the elements of mathematics and of one of the observational or experimental sciences, is likely to have a better and more utilizable brain than he who has a smattering of half a dozen languages and a confused idea of all the " ologies." The habits of mental slovenliness, the illogical thinking, and the incapacity to know when a thing really is mastered and understood, which one so often finds as the results of such an education, are far worse than the narrowness apt to follow the opposite error, which is often associated with the power of accurate logical thought. Those who are deprived of the advantages of a general collegiate education may now, more easily than at any previous period, cultivate mental breadth by reading some of the many excellent general reviews and magazines, and the readable but exact popular expositions now available on nearly all subjects, which are such a feature of our age. Associating, out of working hours, with those whose special pursuits are different from our own is almost necessary to those who would avoid such an asymmetrical development as almost amounts to intellectual deformity.

CHAPTER XXXVIII.

VOICE AND SPEECH.

Voice consists of sounds produced by the vibrations of two elastic bands, the *true vocal cords,* placed in the *larynx,* an upper modified portion of the passage which leads from the pharynx to the lungs. When the vocal cords are put in a certain position, air driven past them sets them in periodic vibration, and they emit a musical note; the lungs and respiratory muscles are, therefore, accessory parts of the vocal apparatus: the strength of the blast produced by them determines the *loudness* of the voice. The larynx itself is the essential voice-organ: its size primarily determines the *pitch* of the voice, which is lower the longer the vocal cords; and, hence, shrill in children, and usually higher pitched in women than in men; the male larynx grows rapidly at commencing manhood, causing the change commonly known as the " breaking of the voice." Every voice, while its general pitch is dependent on the length of the vocal cords, has, however, a certain range, within limits which determine whether it shall be soprano, mezzo-soprano, alto, tenor, baritone, or bass. This variety is produced by muscles within the larynx which alter the tension of the vocal cords. Those characters of voice which we express by such phrases as harsh, sweet, or sympathetic, depend on the structure of the vocal cords of the individual; cords which in vibrating emit only harmonic partial tones (Chap. XXXV) are pleasant; while those in which inharmonic partials are conspicuous are disagreeable.

The vocal cords alone would produce but feeble sounds; those that they emit are strengthened by sympathetic resonance of the air in the pharynx and mouth, the action of which may be compared to that of the sounding-board of a violin. By movements of throat, soft palate, tongue, cheeks, and lips the sounds emitted from the larynx are altered or

supplemented in various ways, and converted into articulate language or *speech.*

The **Larynx** lies in front of the neck, beneath the hyoid bone and above the windpipe; in many persons it is prominent, causing the projection known as "Adam's apple." It consists of a framework of cartilages, partly joined by true synovial joints and partly bound together by membranes;

C₈

Fig. 181.—The more important cartilages of the larynx from behind. *t*, thyroid; *Cs*, its superior, and *Ci*, its inferior, horn of the right side; *ss*, cricoid cartilage; *t*, arytenoid cartilage; *Po*, the corner to which the posterior end of a vocal cord is attached; *Pm*, corner on which the muscles which approximate or separate the vocal cords are inserted; *co*, cartilage of Santorini.

muscles are added which move the cartilages with reference to one another; and the whole is lined by a mucous membrane.

The cartilages of the larynx (Fig. 181) are nine in number; three single and median, and three pairs. The largest (*t*) is called the *thyroid,* and consists of two halves which meet at an angle in front, but separate behind so as to inclose a V-shaped space, in which most of the remaining cartilages lie. The *epiglottis* (not represented in the figure) is fixed to the top of the thyroid cartilage and overhangs the entry from the pharynx to the larynx; it may be seen, covered by mucous membrane, projecting at the base of the tongue, if the latter be pushed down while the mouth is held open in front of a mirror; and is, similarly covered, represented, as seen from behind, at *a* in Fig. 182. The *cricoid,* the last

of the unpaired cartilages, has the shape of a signet-ring; its broad part (**₊₊** , Fig. 181) is on the posterior side and lies at the lower part of the opening between the halves of the thyroid; in front and on the sides it is narrow, and a space, occupied by the *crico-thyroid membrane*, intervenes between its upper border and the lower edge of the thyroid cartilage. The angles of the latter are produced above and below into projecting *horns* (*Cs* and *Ci*, Fig. 181), and the lower horn on each side forms a joint with the cricoid. The thyroid can be rotated on an axis, passing through the joints on each side, and rolled down so that its lower front edge shall come nearer the cricoid cartilage, the membrane there intervening being folded. The *arytenoids* (†, Fig. 181) are the largest of the paired cartilages; they are seated on the upper edge of the posterior wide portion of the cricoid, and form true joints with it. Each is pyramidal with a triangular base, and has on its tip a small nodule (*co*, Fig. 181), the *cartilage of Santorini*. From the tip of each arytenoid cartilage *the aryteno-epiglottidean fold* of mucous membrane (10, Fig. 182) extends to the epiglottis; the cartilage of Santorini causes a projection (8, Fig. 182) in this; and a little farther on (9) is a similar eminence on each side, caused by the remaining pair of cartilages, known as the *cuneiform*, or cartilages of *Wrisberg*.

The **Vocal Cords** are bands of elastic tissue which reach from the inner angle (*Pv*, Fig. 181) of the base of each arytenoid cartilage to the angle on the inside of the thyroid where the sides of the *V* unite; they thus meet in front but are separated at their other ends. The cords are not, however, bare strings, like those of a harp, but covered over with the lining mucous membrane of the larynx, a slit, called the *glottis* (*c*, Fig. 182), being left between them. It is the projecting cushions formed by them on each side of this slit which are set in vibration during phonation. Above each vocal cord is a depression, the *ventricle of the larynx* (*b'*, Fig. 182); this is bounded above by a somewhat prominent edge, *the false vocal cord*. Over most of the interior of the larynx its mucous membrane is thick and covered by ciliated epithelium, and has many mucous glands imbedded in it. Over the vocal cords, however, it is represented only by a thin layer of flat non-ciliated cells, and contains no glands. In quiet breathing, and after death, the free inner edges of the

vocal cords are thick and rounded, and seem very unsuitable for being readily set in vibration. They are also tolerably widely separated behind, the arytenoid cartilages, to which their posterior ends are attached, being separated. Air under

Fig 182.—The larynx viewed from its pharyngeal opening. The back wall of the pharynx has been divided and its edges (11) turned aside. 1, body of hyoid; 2, its small and 3, its great, horns; 4, upper and lower horns of thyroid cartilage; 5, mucous membrane of front of pharynx, covering the back of the cricoid cartilage; 6 upper end of gullet; 7, windpipe, lying in front of the gullet; 8, eminence caused by cartilage of Santorini; 9, eminence caused by cartilage of Wrisberg; both lie in, 10, the *aryteno-epiglottidean fold* of mucous membrane, surrounding the opening (*aditus laryngis*) from pharynx to larynx. *a*, projecting tip of epiglottis, *c*, the glottis, the lines leading from the letter point to the free vibratory edges of the vocal cords. *b'*, the ventricles of the larynx: their upper edges, marking them off from the eminences *b*, are the false vocal cords.

these conditions passes through without producing voice. If they are watched with the laryngoscope during phonation, it is seen that the cords approximate behind so as to narrow the glottis; at the same time they become more tense, and their inner edges project more sharply and form a better-defined margin to the glottis, and their vibrations can be seen. These changes are brought about by the delicately co-

ordinated activity of a number of small muscles, which move the cartilages to which the cords are fixed.

The Muscles of the Larynx. In describing the direction and action of these it is convenient to use the words front or anterior and back or posterior with reference to the larynx itself (that is, as equivalant to ventral and dorsal) and not with reference to the head, as usual. The base of each arytenoid cartilage is triangular and fits on a surface of the cricoid, on which it can slip to and fro to some extent, the ligaments of the joint being lax. One corner of the triangular base is directed inwards and forwards (*i.e.* towards the thyroid) and is called the *vocal process* (*Pv*, Fig. 181), as to it the vocal cords are fixed. The outer posterior angle (*Pm*, Fig. 181) has several muscles inserted on it and is called the *muscular process.* If it be pulled back and towards the middle line the arytenoid cartilage will rotate on its vertical axis, and roll its vocal processes forwards and outwards, and so widen the glottis; the reverse will happen if the muscular process be drawn forwards. The muscle producing the former movement is the *posterior crico-arytenoid* (*Cap*, Fig. 183); it arises from the back of the cricoid cartilage, and narrows to its insertion into the muscular process of the arytenoid on the same side. The opponent of this muscle is the *lateral crico-arytenoid,* which arises from the side of the cricoid cartilage, on its inner surface, and passes upwards and backwards to the muscular process. The posterior crico-arytenoids, working alone, pull inwards and downwards the muscular processes, turn upwards and outwards the vocal processes, and separate the posterior ends of the vocal cords. The lateral crico-thyroid, working alone, pulls downwards and forwards the muscular process, and rotates inwards and upwards the vocal process, and narrows the glottis; it is the chief agent in producing the approximation of the cords necessary for the production of voice. When both pairs of muscles act together, however, each neutralizes the tendency of the other to rotate the arytenoid cartilage; the downward part of the pull of each is, thus, alone left, and this causes the arytenoid to slip downwards and outwards, off the eminence on the cricoid with which it articulates, as far as the loose capsular ligament of the joint will allow. The arytenoid cartilages are thus moved apart and the glottis greatly widened and brought into its state in deep quiet

breathing. Other muscles approximate the arytenoid carti-
lages after the cartilages have been separated. The most im-
portant is the *transverse arytenoid* (*A*, Fig. 183), which runs
across from one arytenoid cartilage to the other. Another is
the *oblique arytenoid* (*Taep*), which runs across the middle
line from the base of one arytenoid to the tip of the other;

thence certain fibres continue in the aryteno-epiglottidean
fold (10, Fig. 182) to the base of the epiglottis; this, with its
fellow, embraces the whole entry to the larynx; when they
contract they bend inwards the tips of the arytenoid car-
tilages, approximate the edges of the aryteno-epiglottidean
fold, and draw down the epiglottis, and so close the passage
from the pharynx to the larynx. When the epiglottis has
been removed, food and drink rarely enter the larynx in
swallowing, the folds of mucous membrane being so brought
together as to effectually close the aperture between them.

Increased tension of the vocal cords is produced by the
crico-thyroid muscles, one of which lies on each side of the
larynx, over the crico-thyroid membrane. Their action may

be understood by help of the diagram, Fig. 184, in which *t* represents the thyroid cartilage, *c* the cricoid, *a* an arytenoid, and *vc* a vocal cord. The muscle passes obliquely backwards and upwards from about *d* near the front end of *c*, to *t*, about *l*, near the pivot (which represents the joint between the cricoid cartilage and the inferior horn of the thyroid). When the muscle contracts it pulls together the anterior ends of *t* and *c*; either by depressing the thyroid (as rep-

Fig. 184.

resented by the dotted lines) or by raising the front end of the cricoid; and thus stretches the vocal cord, if the ary-tenoid cartilages be held from slipping forwards. The antagonist of the crico-thyroid is the *thyro-arytenoid muscle;* it lies, on each side, imbedded in the fold of elastic tissue forming the vocal cord, and passes from the inside of the angle of the thyroid cartilage in front, to the anterior angle and front surface of the arytenoid behind. If the latter be held firm, the muscle raises the thyroid cartilage from the position into which the crico-thyroid pulls it down, and so slackens the vocal cords. If the thyroid be held fixed by the crico-thyroid muscle, the thyro-arytenoid will help to approximate the vocal cords, rotating inwards the vocal processes of the arytenoids.
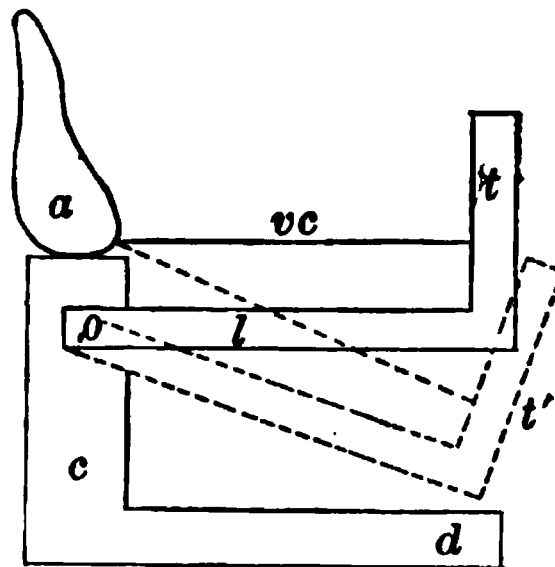
The lengthening of the vocal cords when the thyroid cartilage is depressed tends to lower their pitch; the increased tension, however, more than compensates for this and raises it. There seems, however, still another method by which high notes are produced. Beginning at the bottom of his register, a singer can go on up the scale some distance without a break; but, then, to reach his higher notes, must pause, rearrange his larynx, and begin again. What happens is that, at first, the vocal processes are turned in, so as to approximate but not to meet; the whole length of each edge of the glottis then vibrates, and its tension is increased, and the pitch of the note raised, by increasing contraction of the crico-thyroid. At last this attains its limit and a new method has to be adopted. The vocal processes are more rolled in, until they touch. This produces a node (see

Physics) at that point and shortens the length of vocal cord which vibrates. The shorter string emits a higher note; so the crico-thyroid is relaxed, and then again gradually tightened as the notes sung are raised in pitch from the new starting-point. To pass easily and imperceptibly from one such arrangement of the larynx to another is a great art in singing. There is some reason to believe that a second node may, for still higher notes, be produced at a more anterior point on the vocal cords.

The method of production of *falsetto notes* is uncertain; during their emission the free border of the vocal cords alone vibrates.

The range of the human voice is about three octaves, from *e* (80 vib. per 1″) on the unaccented octave, in male voices, to *c* on the thrice-accented octave (1024 vib. per 1″), in female. Great singers of course go beyond this range; basses have been known to take *a* on the great octave (55 vib. per 1″); and Nilsson in " Il Flauto Magico " used to take *f* on the fourth accented octave (1408 vib. per 1″). Mozart heard at Parma, in 1770, an Italian songstress whose voice had the extraordinary range from *g* in the first accented octave (198 vib. per 1″) to *c* on the fifth accented octave (2112 vib. per 1″). An ordinary good bass voice has a compass from *f* (88 vib. per 1″) to *d″* (297 vib. per 1″); and a soprano from *b′* (248 vib. per 1″) to *g′″* (792).

Vowels are, primarily, compound musical tones produced in the larynx. Accompanying the primary partial of each, which determines its pitch when said or sung, are a number of upper partials, the first five or six being recognizable in good full voices. Certain of these upper partials are reinforced in the mouth to produce one vowel, and others for other vowels; so that the various vowel sounds are really musical notes differing from one another in timbre. The mouth and throat cavities form an air-chamber above the larynx, and this has a note of its own which varies with its size and form, as may be observed by opening the mouth widely, with the lips retracted and the cheeks tense; then gradually closing it and protruding the lips, meanwhile tapping the cheek. As the mouth changes its form the note produced changes, tending in general to pass from a higher to a lower pitch and suggesting to the ear at the same time a change from the sound of ā (father) through ō (more) to ōō

(m*oo*r). When the mouth and throat chambers are so arranged that the air in them has a vibratory rate in unison with any partial in the laryngeal tone, it will be set in sympathetic vibration, that partial will be strengthened, and the vowel characterized by it uttered. As the mouth alters its form, although the same note be still sung, the vowel changes. In the above series (ā, ŏ, ŏŏ) the tongue is depressed and the cavity forms one chamber; for ā this has a wide mouth opening; for ŏ it is narrowed; for ŏŏ still more narrowed, and the lips protruded so as to increase the length of the resonance chamber. The partial tones reinforced in each case are, according to Helmholtz—

In other cases the mouth and throat cavity is partially subdivided, by elevating the tongue, into a wide posterior and a narrow anterior part, each of which has its own note; and the vowels thus produced owe their character to two reinforced partials. This is the case with the series ā (m*a*n), e (th*e*re), and i (mach*i*ne), the tones reinforced by resonance in the mouth being—

The usual ī of English, as in sp*i*re, is not a true simple vowel but a diphthong, consisting of ā (p*a*d) followed by ē (f*ee*t), as may be observed by trying to sing a sustained note to the sound ī; it will then be seen that it begins as ā and ends as ēē. A simple vowel can be maintained pure as long as the breath holds out.

In uttering true vowel sounds the soft palate is raised so as to cut off the air in the nose, which, thus, does not take part in the sympathetic resonance. For some other sounds (the *semi-vowels* or *resonants*) the initial step is, as in the case of the true vowels, the production of a laryngeal tone;

but the soft palate is not raised, and the mouth exit is more or less closed by the lips or the tongue; hence the blast partly issues through the nose, and the air there takes part in the vibrations and gives them a special character; this is the case with *m*, *n*, and *ng*.

Consonants are sounds produced not mainly by the vocal cords, but by modifications of the expiratory blast on its way through the mouth. The current may be interrupted and the sound changed by the lips (*labials*); or, at or near the teeth, by the tip of the tongue (*dentals*); or, in the throat, by the root of the tongue and the soft palate (*gutturals*). Consonants are also characterized by the kind of movement which gives rise to them. In *explosives* an interruption to the passage of the air-current is suddenly interposed or removed (P, T, B, D, K, G). Other consonants are *continuous* (as F, S, R), and may be subdivided into—(1) *aspirates*, characterized by the sound produced by a rush of air through a narrow passage, as when the lips are approximated (F), or the teeth (S), or the tongue is brought near the palate (Sh), or its tip against the two rows of teeth, they not being quite in contact (Th). For L the tongue is put against the hard palate and the air escapes on its sides. For Ch (as in the proper Scotch pronunciation of *loch*) the passage between the back of the tongue and the soft palate is narrowed. To many of the above pure consonants answer others, in whose production true vocalization (*i.e.* a laryngeal tone) takes a part. F with some voice becomes V; S becomes Z, Th soft (tee*th*) becomes Th hard; and Ch becomes Gh. (2) *resonants;* these have been referred to above. (3) *vibratories* (the different forms of R), which are due to vibrations of parts bounding a constriction put in the course of the air-current. Ordinary R is due to vibrations of the tip of the tongue held near the hard palate; and guttural R to vibrations of the uvula and parts of the pharynx.

The consonants may physiologically be classified as in the following table (Foster):

Explosives. *Labials*, without voice.....P.
" with voice ....B.
Dentals, without voice.....T.
" with voice........D.
Gutturals, without voice...K.
" with voice......G (hard).

Aspirates. *Labials,* without voice......F.

" with voice........V.

Dentals, without voice.....S, L, Sh, Th (hard).

" with voice........Z, Zh (azure), Th (soft).

Gutturals, without voice...Ch (loch).

" with voice .....Ch.

Resonants. *Labial*....................M.

Dental... ....N.

Guttural..................NG.

Vibratories. *Labial*—not used in European languages.

Dental.....................R (common).

Guttural..................R (guttural).

H is a laryngeal sound: the vocal cords are separated for its production, yet not so far as in quiet breathing. The air-current then produces a friction sound but not a true note, as it passes the glottis; and this is again modified when the current strikes the wall of the pharynx. Simple sudden closure of the glottis, attended with no sound, is also a speech element, though we do not indicate it with a special letter, since it is always understood when a word begins with a vowel, and only rarely is used at other times. The Greeks had a special sign for it, ', the *soft breathing;* and another, ', the *hard breathing,* answering somewhat to our *h* and indicating that the larynx was to be held open, so as to give a friction sound, but not voice.

In whispering there is no true voice; the latter implies true *tones,* and these are only produced by periodic vibrations; whispering is a *noise.* To produce it the glottis is considerably narrowed but the cords are not so stretched as to produce a sharply defined edge on them, and the air driven past is then thrown into irregular vibrations. Such vibrations as coincide in period with the air in the mouth and throat are always present in sufficient number to characterize the vowels; and the consonants are produced in the ordinary way, though the distinction between such letters as P and B, F and V, remains imperfect.

CHAPTER XXXIX.

REPRODUCTION.

Reproduction in General. In all cases reproduction consists, essentially, in the separation of a portion of living matter from a parent; the separated part bearing with it, or *inheriting*, certain tendencies to repeat, with more or less variation, the life history of its progenitor. In the more simple cases a parent merely divides into two or more pieces, each resembling itself except in size; these then grow and repeat the process; as, for instance, in the case of Amœba and our own white blood corpuscles (pp. 23, 44). Such a process may be summed up in two words as *discontinuous growth;* the mass, instead of increasing in size without segmentation, divides as it grows, and so forms independent living beings. In some tolerably complex multicellular animals we find essentially the same thing; at times certain cells of the fresh-water Polype multiply by simple division in the manner above described, but there is a certain concert between them: they build up a tube projecting from the side of the parent, a mouth-opening forms at the distal end of this, tentacles sprout out around it, and only when thus completely built up and equipped is the young Hydra set loose on its own career. How closely such a mode of multiplication is allied to mere growth is shown by other polypes in which the young, thus formed, remain permanently attached to the parent stem, so that a compound animal results. This mode of reproduction (known as *gemmation* or *budding*) may be compared to the method in which many of the ancient Greek colonies were founded; carefully organized and prepared at home, they were sent out with a due proportion of artificers of various kinds; so that the new commonwealth had from its first separation a considerable division of employments in it, and was, on a small scale, a repetition of the parent community. In the great majority of animals, however (even those which at times multiply by budding), a different mode of reproduction

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occurs, one more like that by which our western lands were settled and gradually built up into Territories and States. The new individual in the political world began with little differentiation; it consisted of units, separated from older and highly organized societies, and these units at first did pretty much everything, each man for himself, with more or less efficiency. As growth took place development also occurred; persons assumed different duties and performed different work until, finally, a fully organized State was formed. Similarly, the body of one of the higher animals is, at an early stage of life, merely a collection of undifferentiated cells, each capable of multiplication by division, and more or less retaining all its original protoplasmic properties; and with no specific individual endowment or function. The mass (Chap. III.) then slowly differentiates into the various tissues, each with a predominant character and duty; at the same time the majority of the cells lose their primitive powers of reproduction, though exactly how completely is a problem not yet sufficiently studied. In adult Vertebrates it seems certain that the white blood corpuscles multiply by division: and in some cases (in the newts or tritons, for example) a limb is reproduced after amputation. But exactly what cells take part in such restorative processes is uncertain; we do not know if the old bone corpuscles left form new bones, old muscle-fibres new muscles, and so on; though it is probable that the little-differentiated leucocytes build up most of the new limb. In Mammals no such restoration occurs; an amputated leg may heal at the stump but does not form again. In the healing processes the connective tissues play the main part, as we might expect; their cellular elements being but little modified from their primitive state (p. 102) can still multiply and develop. New blood capillaries, however, sprout out from the sides of old, and new epidermis seems only to be formed by the multiplication of epidermic cells; hence the practice, frequently adopted by surgeons, of transplanting little bits of skin to points on the surface of an extensive burn or ulcer. In blood capillaries and epidermis the departure from the primary undifferentiated cell is but slight; and, as regards the cuticle, one of the permanent physiological characters of the cells of the *rete mucosum* is their multiplication throughout the whole of life; that is a main physiological characteristic of the tissue: the same is very probably

true of the protoplasmic cells forming the walls of the capillaries. When a highly differentiated tissue is replaced in the body of mammals after breaking down or removal, it is usually by the activity of special cells set apart for that purpose, or by repair or outgrowth of the cells affected and not by their division. The red blood corpuscles are constantly being broken down and replaced, but the new ones are not formed by the division of already fully formed corpuscles but by certain special *hæmatoblastic cells* retained throughout life in the red marrow of bone and perhaps in the spleen. The nervous tissues are highly differentiated and a nerve is often regenerated after division, but this is by outgrowth of the ends of axis cylinders still attached to their cells and by secondary formation of a medullary sheath around these, and not by division or multiplication of already existing fibres. A striped muscle when cut across is healed by the formation of a band of connective tissue; after a very long time it is said that true muscular fibres may be found in the cicatrix, but their origin is not known; it is probably not from previously developed muscle fibres. On the other hand, the less differentiated unstriated muscle has been observed to be repaired in some cases after injury by true karyokinetic division of previously formed muscle cells. Although many gland-cells in the performance of their physiological work are partially broken down and lost in their secretion, and then repaired by the residue of the cell, multiplication by division of fully differentiated gland-cells does not appear to occur, if we except such organs as the testes, the secretion of which consists essentially of cells. An excised portion of a salivary or parotid gland is never regenerated: the wound is repaired by connective tissues.

We find, then, as we ascend in the animal scale a diminishing reproductive power in the tissues generally: with the increasing division of physiological labor, with the changes that fit pre-eminently for one work, there is a loss of other faculties, and this one among them. The more specialized a tissue the less the reproductive power of its elements, and the most differentiated tissues are either not reproduced at all after injury, or only by the specialization of amœboid cells, and not by a progenitive activity of survivors of the same kind as those destroyed. In none of the higher animals, therefore, do we find multiplication by simple division, or by budding: no one

cell, and no group of cells used for the physiological maintenance of the individual, can build up a new complete living being; but the continuance of the race is specially provided for by setting apart certain cells which shall have this one property—cells whose duty is to the species and not to any one representative of it—an essentially altruistic element in the otherwise egoistic whole.

Sexual Reproduction. In some cases, especially among insects, the specialized reproductive cells can develop, each for itself, under suitable conditions, and give rise to new individuals; such a mode of reproduction is called *parthenogenesis:* but in the majority of cases, and always in the higher animals, this is not so; the fusion of two cells, or of products of two cells, is a necessary preliminary to development. Commonly the coalescing cells differ considerably in size and form, and one takes a more direct share in the developmental processes; this is the egg-cell or *ovum;* the other is the *sperm-cell* or spermatozoön. The fusion of the two is known as *fertilization.* Animals producing both ova and spermatozoa are *hermaphrodite;* those bearing ova only, *female;* and those spermatozoa only, *male:* hermaphroditism is not found in Vertebrates, except in rare and doubtful cases of monstrosity.

Accessory Reproductive Organs. The organ in which ova are produced is known as the *ovary,* that forming spermatozoa, as the *testis* or *testicle;* but in different groups of animals many additional accessory parts may be developed. Thus, in all but the very lowest Mammalia, the offspring is nourished for a considerable portion of its early life within the body of its mother, a special cavity, the *uterus* or *womb,* being provided for this purpose: the womb communicates with the exterior by a passage, the *vagina;* and two tubes, the *oviducts* or *Fallopian tubes,* convey the eggs to it from the *ovaries.* In addition, *mammary glands* provide milk for the nourishment of the young in the first months after birth. In the male mammal we find as accessory reproductive organs, *vasa deferentia* which convey from the testes the seminal fluid containing spermatozoa; *vesiculæ seminales* (not present in all Mammalia), glands whose secretion is mixed with that of the testes or is expelled after it in the sexual act; a *prostate gland,* whose secretion is added to the semen; and an erectile organ, the *penis,* by which the fertilizing liquid is conveyed into the vagina of the female.

The Male Reproductive Organs. The testes in man are paired tubular glands, which lie in a pouch of skin called the *scrotum.* This pouch is subdivided internally by a partition into right and left chambers, in each of which a testicle lies. The chambers are lined inside by a serous membrane, the *tunica vaginalis*, and this doubles back (like the pleura round the lung) and covers the exterior of the gland. Between the external and reflected layers of the tunica vaginalis is a space containing a small quantity of lymph.

The testicles develop in the abdominal cavity, and only later (though commonly before birth) descend into the scrotum, passing through apertures in the muscles, etc., of the abdominal wall, and then sliding down over the front of the pubes, beneath the skin. The cavity of the tunica vaginalis at first is a mere offshoot of the peritoneal cavity, and its serous membrane is originally a part of the peritoneum. In the early years of life the passage along which the testis passes usually becomes nearly closed up, and the communication between the peritoneal cavity and that of the tunica vaginalis is also obliterated. Traces of this passage can, however, readily be observed in male infants; if the skin inside the thigh be tickled a muscle lying beneath the skin of the scrotum is made to contract reflexly, and the testis is jerked up some way towards the abdomen and quite out of the scrotum. Sometimes the passage remains permanently open and a coil of intestine may descend along it and enter the scrotum, constituting an *inguinal hernia or rupture.* A *hydrocele* is an excessive accumulation of liquid in the serous cavity of the tunica vaginalis.

Beneath its covering of serous membrane each testis has a proper fibrous tunic of its own. This forms a thick mass on the posterior side of the gland, from which partitions or *septa* (*i*, Fig. 185) radiate, subdividing the gland into many chambers. In each chamber

Fig. 185.—Diagram of a vertical section through the testis. *a, a,* tubuli seminiferi; *b,* vasa recta; *d,* vasa efferentia ending in the coni vasculosi; *e, e,* epididymis. *h,* vas deferens.

lie several greatly coiled *seminiferous tubules, a, a,* averaging in length 0.68 metre (27 inches) and in diameter only 0.14 mm. ($\frac{1}{180}$ inch). Their total number in each gland is about 800.

Near the posterior side of the testis the tubules unite to form about 20 *vasa recta* (*b*), and these pass out of the gland at its upper end, as *the vasa efferentia* (*d*), which become coiled up into conical masses, the *coni vasculosi;* these, when unrolled, are tubes from 15 to 20 cm. (6–8 inches) in length; they taper somewhat from their commencements at the vasa efferentia, where they are 0.5 mm. ($\frac{1}{50}$ inch) in diameter, to the other end where they terminate in the *epididymis* (*e, e*, Fig. 185). The latter is a narrow mass, slightly longer than the testicle, which lies along the posterior side of that organ, near the lower end of which it passes (*g*) into the *vas deferens, h.* If the epididymis be carefully unravelled it is found to consist of a tube about 6 metres (20 feet) in length, and varying in diameter from 0.35 to 0.25 mm. ($\frac{1}{70}$ to $\frac{1}{90}$ inch).

The *vas deferens* (*h*, Fig. 185) commences at the lower part of the epididymis as a coiled tube, but it soon ceases to be convoluted and passes up beneath the skin covering the inner part of the groin, till it gets above the pelvis and then, passing through the abdominal walls, turns inwards, backwards, and downwards, to the under side of the urinary bladder, where it joins the duct of the seminal vesicle; it is about 0.6 meters (2 feet) in length and 2.5 mm. ($\frac{1}{10}$ inch) in diameter. Its lining epithelium is ciliated.

The *vesiculæ seminales*, two in number, are membranous receptacles which lie, one on each side, beneath the bladder, between it and the rectum. They are commonly about 5 cm. (2 inches) long and a little more than a centimetre wide (or about 0.5 inch) at their broadest part. The narrowed end of each enters the vas deferens on its own side, the tube formed by the union being the *ejaculatory duct*, which, after a course of about an inch, enters the urethra near the neck of the bladder. In some animals the *vesiculæ seminales* form a liquid which is added to the secretion of the testis. In man they appear to be merely reservoirs in which the semen collects.

The *prostate gland* is a dense body, about the size of a large chestnut, which surrounds the commencement of the urethra; the ejaculatory ducts pass through it. It is largely made up of fibrous and unstriped muscular tissues, but contains also a number of small secreting saccules whose ducts open into the urethra. The prostatic secretion though small in amount would appear to be of importance: at least the gland remains undeveloped in persons who have been castrated

in childhood; and atrophies after removal of the testicles later in life.

The *male urethra* leads from the bladder to the end of the penis, where it terminates in an opening, *the meatus urinarius.* It is described by anatomists as made up of three portions, the prostatic, the membranous, and the spongy. The first is surrounded by the prostate gland and receives the ejaculatory ducts. On its posterior wall, close to the bladder, is an elevation containing erectile tissues (see below) and supposed to be dilated during sexual congress, so as to cut off the passage to the urinary receptacle. On this crest is an opening leading into a small recess, the *utricle,* which is of interest, since the study of its embryology shows it to be an undeveloped male uterus. The succeeding membranous portion of the urethra is about 1.8 cm. (¾ inch) long; the spongy portion lies in the penis.

The *penis* is composed mainly of *erectile tissue, i.e.,* tissues so arranged as to inclose cavities which can be distended by blood. Covered outside by the skin, internally it is made up of three elongated cylindrical masses, two of which, the *corpora cavernosa,* lie on its anterior side; the third, the *corpus spongiosum,* surrounds the urethra and lies on the posterior side of the organ for most of its length; it, however, alone forms the terminal dilatation, or *glans,* of the penis. Each *corpus cavernosum* is closely united to its fellow in the middle line and extends from the pubic bones, to which it is attached behind, to the glans penis in front. It is enveloped in a dense connective-tissue capsule from which numerous bars, containing white fibrous, elastic, and unstriped muscular tissues, radiate and intersect in all directions, dividing its interior into many irregular chambers called *venous sinuses.* Into these blood is conveyed partly through open capillaries, partly directly by the open ends of small arteries; this blood is carried off by veins proceeding from the sinuses.

The arteries of the penis are supplied with vaso-dilator nerves, the *nervi erigentes,* derived from the sacral plexus. Under certain conditions these are stimulated and, the arteries expanding, blood is poured into the venous sinuses faster than the veins drain it off; the latter are probably also at the same time compressed where they leave the penis by the contraction of certain muscles passing over them. Simultaneously the involuntary muscular tissue of the bars ramify-

ing through the erectile masses relaxes. As a result the whole organ becomes distended and finally rigid and erect. The co-ordinating *centre of erection* lies in the lumbar region of the spinal cord, and may be excited reflexly by mechanical stimulation of the penis, or under the influence of nervous impulses originating in the brain and associated with sexual emotions. The corpus spongiosum resembles the corpora cavernosa in essential structure and function.

The skin of the penis is thin and forms a simple layer for some distance; towards the end of the organ it separates and forms a fold, the *foreskin* or *prepuce*, which doubles back, and, becoming soft, moist, red, and very vascular, covers the glands to the *meatus urinarius*, where it becomes continuous with the mucous membrane of the urethra; in it, near the projecting posterior rim of the glans, are imbedded many sebaceous glands. It possesses nerve end organs (*genital corpuscles*) which much resemble end bulbs in structure.

The Seminal Fluid. The essential elements of the testicular secretion are much modified cells, the *spermatozoa*, which are passed out with some albuminous liquid. The spermatozoa (Fig. 186) are motile bodies about 0.04 m.m. ($\frac{1}{500}$ inch) in length. They have a flattened clear *body* or *head* and a long vibratile *tail* or cilium; the portion of the tail nearest to the head is thicker than the rest, and is known as the *neck*. The mode of development of a spermatozoön shows that the head is a cell-nucleus and the neck and tail a modified cell-body.
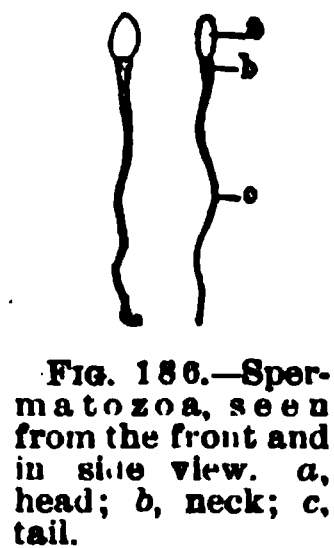
FIG. 186.—Spermatozoa, seen from the front and in side view. *a*, head; *b*, neck; *c*, tail.

On cross-section a seminiferous tubule presents externally a well-marked basement membrane, upon which are borne several layers of cells; the lumen or bore of the tubule is in great part occupied by the tails of spermatozoa projecting from some of the lining cells. The outer cells, those next the basement membrane, are arranged in a single layer, and are usually found in one or other stage of active karyokinetic division (p. 19). The result of the division is an outer cell, which remains next the basement membrane to repeat the process, and an inner, which is the *mother-cell* of spermatozoa. The latter cell by repeated mitotic division give rise to a number of cells lying side by side and each having a relatively large nucleus and small cell-body. These

cells elongate, the nucleus remaining near the deeper end and the protoplasm extending towards the lumen of the tubule, into which it ultimately projects. Such cells are *spermatoblasts*, and lie in bunches side by side and several rows deep. Interlaced among them are other granular supporting cells of the epithelium, which are probably concerned with the nutrition of the essential cells. The final step by which the spermatoblast is converted into a spermatozoön is a karyokinetic division into two unequal cells: a part of the nucleus with a little of the protoplasm separates and appears to have no further function; the remaining part of the nucleus (*male pronucleus*) remains as the head of the spermatozoön and the cell protoplasm develops into the neck and tail. The spermatozoa appear frequently to be cast off before their development is completed: at least many spermatoblasts which have not gone through the final stages are found in the vasa recta, and even in the vas deferens. Probably the secretion normally collects in the vesiculae seminales, and there undergoes its final elaboration.

The **Reproductive Organs of the Female.** Each ovary (*o*, Fig. 187) is a dense oval mass about 3.25 cm. (1.5 inches) in length, 2 cm. (0.75 inch) in width, and 1.27 cm. (0.5 inch) in thickness; it weighs from 4 to 7 grams (60–100 grains). The organs lie in the pelvic cavity enveloped in a fold of peritoneum (the *broad ligament*), and receive blood-vessels and nerves along one border. From time to time ova reach the surface, burst through the enveloping peritoneum, and are received by the wide fringed aperture, *fi*, of the oviduct or Fallopian tube, *od*. This tube narrows towards its inner end, where it communicates with the uterus, and is lined by a mucous membrane, covered by ciliated epithelium; plain muscular tissue is also developed in its wall. The *uterus* (*u*, *c*, Fig. 187) is a hollow organ, with relatively thick muscular walls (left unshaded in the figure); it contains the foetus during pregnancy and expels it at birth; it lies in the pelvis between the urinary bladder and the rectum (Fig. 188); the Fallopian tubes open into its anterior corners. It is free above, but its lower end is attached to and projects into the vagina. In the fully developed virgin state the organ is somewhat pear-shaped, but flattened from before back; about 7.5 cm. (3 inches) in length, 5 cm. (2 inches) in breadth at its upper widest part, and 2.5 cm. (1 inch) in thickness; it

or partly-dividing eggs. In all the higher mammalia the dentoplasm is relatively sparse and tolerably evenly mingled with the protoplasm, and the whole fertilized ovum divides to form the first cells of the embryo: such eggs are named *holoblastic.*

The Maturation of the Ovum. From time to time, usually at intervals of about four weeks, in a woman of child-bearing age, certain ova after attaining the size and structure described in the preceding paragraph undergo further changes by which the egg-cell is rendered capable of fertiliza tion. These phenomena, known as the *maturation of the ovum*, result in separation of small parts of the nucleus or germinal vesicle and cell protoplasm from the rest. They are essentially typical cases of indirect cell division (p. 19). The cell-body shrinks a little so as to not quite fill the zona pellu-cida, and the germinal vesicle approaches one side. Meanwhile the nuclear membrane and karyoplasm form the chromatic loop and this divides into the usual two sets of V s. One set of these, with part of the nuclear plasm, now separates with a little of the cell protoplasm to form a small cell, the *first polar globule* or *directive corpuscle* (*c*, Fig 191). The much larger cell result ing from the division and represent-ing the remainder of the vitellus and nucleus now repeats the process, and gives rise to the *second polar globule.* In Fig. 191 the first polar globule is shown at *c*, as already separated, and the nucleus, *d*, is dividing, preparatory to the forma-tion of the second directive cor-puscle. The stage of karyokinesis is more advanced than those repre-sented in Fig. 10. The two polar globules lie for a time (Fig. 192) within the zona pellucida, in the space left by the shrinkage of the vitellus, but take no part in the formation of the embryo and soon disappear. The rest of the original ovum is now mature and ready for fertili-zation; its nucleus is known as the *female pronucleus, fn,* Fig. 192. It passes towards the centre of the ovum and forms

FIG. 191.—An ovum about to form the second polar globule. *a*, zona pellucida ; *b*, space filled with liquid and left by the shrink-age of the vitellus; *c*, first polar globule, *d*, nucleus of ovum divid-ing preparatory to the separation of the second polar globule; *v*, vitellus, showing radial arrange-ment of its granules near the end of the nuclear spindle.

the usual recticulum of karyoplasm found in normal resting nuclei (Fig. 8).

Ovulation. From puberty, during the whole child-bearing period of life, certain comparatively very large Graafian follicles may nearly always be found either close to the surface of the ovary or projecting on its exterior. These, by accumulation of liquid within them, have become distended to a diameter of about 4 mm. (⅙ inch); finally, the thinned projecting portion of the wall of the follicle, which differs from the rest in containing few blood-vessels, gives way and the ovum is discharged, surrounded by some cells of the discus proligerus. The emptied follicle becomes filled up with a reddish-yellow mass of cells, and constitutes the *corpus luteum*, which recedes again to the interior of the ovary and disappears in three or four weeks, unless pregnancy occur; in that case the corpus luteum increases for a time, and persists during the greater part of the gestation period.

Menstruation. Ovulation occurs during the sexual life of a healthy woman at intervals of about four weeks, and is attended with important changes in other portions of the generative apparatus. The ovaries and Fallopian tubes become congested, and the fimbriæ of the latter are erected and come into contact with the ovary so as to receive any ova discharged. Whether the fimbriæ embrace the ovary and catch the ovum, or merely touch it at various points and the ova are swept along them by their cilia to the cavity to the oviduct, is not certain. Having entered the Fallopian tube the egg slowly passes on to the uterus, probably moved by the cilia lining the oviduct; its descent pro' bly takes about four or five days; if not fertilized, it dies and is passed out. In the womb important changes occur at or just before the periods of ovulation; its mucous membrane becomes swollen and soft, and minute hemorrhages occur in its substance. The superficial layers of the uterine mucous membrane are broken down, and discharged along with more or less blood, constituting the *menses*, or monthly sickness, which commonly lasts from three to five days. During this time the vaginal secretion is also increased, and, mixed with the blood discharged, more or less alters its color and usually destroys its coagulating power. Except during pregnancy and while suckling, menstruation occurs at the above intervals, from puberty up to about the forty-fifth year; the periods then become irregular, and finally the discharges cease; this

is an indication that ovulation has come to an end, and that the sexual life of the woman is completed. This time, the *climacteric* or " turn of life," is a critical one; various local disorders are apt to supervene, and even mental derangement.

Hygiene of Menstruation. During menstruation there is apt to be more or less general discomfort and nervous irritability; the woman is not quite herself, and those responsible for her happiness ought to watch and tend her with special solicitude, forbearance, and tenderness, and protect her from anxiety and agitation. Any strong emotion, especially of a disagreeable character, is apt to check the flow, and this is always liable to be followed by serious consequences. A sudden chill often has the same effect; hence a menstruating woman ought always to be warmly clad, and take more than usual care to avoid draughts or getting wet. At these periods, also, the uterus is enlarged and heavy, and being (as may be seen in Fig. 188) but slightly supported, and that near its lower end, it is especially apt to be displaced or distorted; it may tilt forwards or sideways (*versions of the uterus*), or be bent where the neck and body of the organ meet (*flexion*). Hence violent exercise at this time should be avoided, though there is no reason why a properly clad woman should not take her usual daily walk.

The absence of the menstrual flow (*amenorrhœa*) is normal during pregnancy and while suckling; and in some rare cases it never occurs throughout life, even in healthy women capable of child-bearing. Usually, however, the non-appearance of the menses at the proper periods is a serious symptom, and one which calls for prompt measures. In all such cases it cannot be too strongly impressed upon women that the most dangerous thing to do is to take drugs tending to induce the discharge, except under skilled advice; to excite the flow, in many cases, as for example occlusion of the os uteri, or in general debility (when its absence is a conservative effort of the system), may have the most disastrous results.

Fertilization. As the ovum descends the Fallopian tube the changes of menstruation are taking place in the uterus. Fertilization usually takes place in a Fallopian tube. The spermatozoa are carried along partly, perhaps, by the contractions of the muscular walls of the female cavities, but mainly by their own activity. Occasionally the ovum is fertilized

before reaching the Fallopian tube and fails to enter it, giving rise to an *extra-uterine pregnancy.*

The actual process of the fertilization of the ovum has only been observed in the lower animals, but there is no doubt that the phenomena are the same in all essentials in all cases. Some of the spermatozoa penetrate the zona pellucida and the head of one of them enters the ovum, when it grows and forms the male pronucleus (*mn*, Fig. 192). This travels towards the nucleus of the matured ovum or female pronucleus, *fn*, and in each pronucleus a karyoplastic filament forms and breaks up into a set of V's; in the pronuclei represented in Fig. 192 this has not yet taken place, the karyoplasm being still arranged in a reticulum. The tail of the spermatozoön (which represents, it will be remembered, the protoplasm of a male cell) disappears; whether it is cast off when the head enters the vitellus or mingles with the protoplasm of the

FIG. 192.—An ovum shortly before the fusion of the pronuclei. *a*, zona pellucida, *b*, polar globules; *fn*, female pronucleus; *mn*, male pronucleus; *pp*, attraction bodies, with the nuclear spindle lying between them; *s*, spermatozoa which have not taken part in fertilization.

latter is not known. As the pronuclei approach one another two attraction particles, *p*, *p*, appear in the protoplasm of the ovum; around these the granules of the vitellus show a radial arrangement and a nuclear spindle (p. 19) unites them. The spindle lies with its long axis at right angles to a line joining the pronuclei. The latter next completely fuse across the middle of the spindle and form a new single nucleus. Fertilization is then complete, and the ovum capable of dividing or segmenting (Fig. 11) to form the cells which by multiplication and differentiation build up the embryo. The zona pellucida takes no part in the segmentation and is gradually absorbed.

The Signification of the Polar Globules. The union of the male and female pronuclei is the essential fact in fertilization and the material basis of all the phenomena of heredity; therefore everything pertaining to it is of very great interest. There is reason to believe that each half of the nucleus of the fertilized egg contains karyoplasm from both pronuclei, and that in all subsequent cell-divisions each new cell gets nuclear

karyoplasm from both, and therefore contains both male and female morphological elements. If this be so, every cell of the adult Body contains a material representative of both father and mother, and may be regarded as hermaphrodite. Upon this supposition explanations of the unequal cell-divisions of the ovum giving rise to the polar globules have been based. The ovum before maturation and the spermatoblast before final formation of the spermatozoön being bisexual, each must, it has been suggested, get rid of material derived from one parent before it can fuse with a residuum of the other to make a new cell. The spermatoblast therefore in its first cell-division separates female nuclear matter, and the spermatozoön is a purely male cell; the ovum on the other hand gets rid of male material in the polar globules, and the mature ovum is a solely female cell; the union of the two makes a complete hermaphrodite cell from which the new animal develops. This view was supported by the belief that certain insect eggs which develop parthenogenetically did not separate polar globules before commencing to form the embryo. It is now known, however, that such eggs do separate *one* polar globule, so the theory requires modification. We cannot here go into the discussion of this matter, which is one of the most interesting biological questions. The argument gathers mainly round the theory (Weismann) that each complete cell apart from male and female elements contains two kinds of living material: one (*nuclear plasma*) with controlling, reproducing, and hereditary functions; the other (*nutritive plasma*) with assimilative duties and other powers in various cells, as contractility, irritability, and so forth, but exercising these under the influence and direction of the nuclear plasma. In the nuclear plasma itself are two distinct substances—a *germinal plasma* with hereditary functions, and alone found in the just fertilized ovum, and a *histogenetic* or *tissue-building plasma*, which is formed by and from the germinal plasma and controls cell-growth, division, and differentiation. The ovum in the first polar globule gets rid of some of its histogenetic plasma, and then in the second polar globule of the male portion of its germinal plasma, and these are replaced by the material brought by the spermatozoön, which is a cell that has in a similar way got rid of some of its histogenetic and germinal plasma. On this theory, moreover, the proportion of the ovum extruded in the polar globules and the ratio of that

remaining to the germ plasma brought by the spermatozoön may be supposed to differ in different instances and account for individual differences in the offspring: thus some physical basis for the facts of *variation* as well as of heredity would be obtained.

Impregnation. The fertilized ovum continues its descent to the uterine cavity, but, instead of lying dormant like the unfertilized, segments (p. 29), and forms a morula. This, entering the womb, becomes imbedded in the soft, vascular mucous membrane from which it imbibes nourishment, and which, instead of being cast off in subsequent menstrual discharges, is retained and grows during the whole of pregnancy, having important duties to discharge in connection with the nutrition of the embryo.

Sexual congress is most apt to be followed by pregnancy if it occur immediately after a menstrual period; at those times a ripe ovum is usually in the Fallopian tube, near the upper end of which it is probably fertilized in the majority of cases. There is some difference of opinion as to whether the rupture of the Graafian follicle occurs most frequently immediately before the appearance of the menstrual flow, or towards its close; but the preponderance of evidence favors the latter view. The menstrual process probably is a special preparation of the womb for the reception of an embryo and its nourishment. There is, however, evidence that ova are ocasionally discharged at other than the regular monthly periods of ovulation and may be fertilized and cause a pregnancy.

Pregnancy. When the mulberry mass reaches the uterine cavity the mucous membrane lining the latter grows rapidly and forms a new, thick, very vascular lining to the womb, known as the *decidua*. At one point on this the morula becomes attached, the decidua growing up around it. As pregnancy advances and the embryo grows, it bulges out into the uterine cavity and pushes before it that part of the decidua which has grown over it (the *decidua reflexa*); at about the end of the third month this coalesces with the decidua lining the opposite sides of the uterine cavity so that the two can no longer be separated. That part of the decidua (*decidua serotina*) against which the morula is first attached subsequently undergoes a great development in connection with the formation of the placenta (see below). Meanwhile the whole uterus enlarges; its muscular coat especially thickens. At first the

organ still lies within the pelvis, where there is but little room for it; it accordingly presses on the bladder and rectum (see Fig. 188) and the nerves in the neighborhood, frequently causing considerable discomfort or pain; and, reflexly, often exciting nausea or vomiting (the *morning sickness* of pregnancy). Later on, the pregnant womb escapes higher into the abdominal cavity, and although then larger, the soft abdominal walls more readily make room for it, and less discomfort is usually felt, though there may be shortness of breath and palpitation of the heart from interference with the diaphragmatic movements. All tight garments should at this time be especially avoided; the woman's breathing is already sufficiently impeded, and the pressure may also injure the developing child. Meanwhile, changes occur elsewhere in the Body. The breasts enlarge and hard masses of developing glandular tissue can be felt in them; and there may be mental symptoms: depression, anxiety, and an emotional nervous state.

During the whole period of gestation the woman is not merely supplying from her blood nutriment for the fœtus, but also, through her lungs and kidneys, getting rid of its wastes; the result is a strain on her whole system which, it is true, she is constructed to bear and will carry well if in good health, but which is severely felt if she be feeble or suffering from disease. The healthy married woman who endeavors to evade motherhood because she thinks she will thus preserve her personal appearance, or because she dislikes the trouble of a family, deserves but little sympathy; she is trying to escape a duty voluntarily undertaken, and owed to her husband, her country, and her race; but she whose strength is undermined and whose life is made one long discomfort for the sexual gratification of her husband deserves every consideration, and the family physician ought perhaps to warn the husband more frequently than he does of the risk to a delicate wife's health, or even life, of frequent pregnancies: and the husband should control himself accordingly. The professor of gynæcology in a leading medical school, gives it as his deliberate opinion that the majority of American women must at some periods of their lives choose between freedom from pregnancy or early death.

Apart from pregnancy, moreover, a woman's health is often injured by frequent sexual intercourse. A physician who has unusual opportunities of knowing states that he has reason to

believe that not only is the act of sexual congress at best, from a physical point of view, a mere nuisance to the majority of women belonging to the more luxurious classes of society after they attain the age of twenty-two or twenty-three, but that a very considerable proportion suffer acute pain from it such as, if frequent, breaks down the general health. A loving woman, finding her highest happiness in suffering for those dear to her, is very unlikely to let her husband know this, so long as she can bear it; but if the possibility is known it will not, perhaps, need much acuteness in him to discover such suffering when it exists, nor very much real affection to direct himself accordingly. In the class of cases referred to, rest of the over-irritable and congested female organs is above all essential. The cause is frequently removable by simple, but skilled, treatment; the desirability of rendering this available to a woman in members of her own sex is now generally recognized.

The Intra-Uterine Nutrition of the Embryo. At first the embryo is nourished by absorption of materials from the soft vascular lining of the womb; as it increases in size this is not sufficient, and a new organ, the *placenta*, is formed for the purpose. A fœtal outgrowth, the *allantois*, plants itself firmly against the *decidua serotina*, and villi developed on it burrow from its surface into the uterine mucous membrane. In the deeper layer of this latter are large sinuses through which the maternal blood flows, and into which the allantoic villi project. Blood is brought from the fœtus to the allantois by arteries and carried back by veins after traversing the capillaries of the villi, and while flowing through these receives, by dialysis, oxygen and food materials from the maternal blood, and gives up to it carbon dioxide, urea, and other wastes. There is thus no direct intermixture of the two bloods; the embryo is from the first an essentially separate and independent organism. The allantois and decidua serotina becoming inseparably united together form the placenta, which in the human species is, when fully developed, a round thick mass about the size of a large saucer, connected to the embryo by a narrow stalk, the *umbilical cord*, in which blood-vessels run to and from the placenta.

Parturition. At the end of from 275 to 280 days from fertilization of the ovum (*conception*) pregnancy terminates, and the child is expelled by powerful contractions of the

uterus, assisted by those of the muscles in the abdominal walls. When the child is born, it has attached to its navel the umbilical cord. which is then usually ligatured and cut across: some good authorities, however, maintain that this should not be done until after the contractions which expel the placenta, as otherwise a quantity of the infant's blood remains in that organ; the loss of which might be serious to a feeble infant. Shortly after the birth of the child renewed uterine contractions detach and expel the placenta, both its fœtal or allantoic and maternal or decidual part, as the *after-birth.* Where it is torn loose from the uterine wall large blood sinuses are left open; hence a certain amount of bleeding occurs, but in normal labor this is speedily checked by firm contraction of the uterus. Should this fail to take place profuse hæmorrhage occurs (*flooding*) and the mother may bleed to death in a few minutes unless prompt measures are adopted.

For a few days after delivery there is some discharge (the *lochia*) from the uterine cavity: the whole decidua being broken down and carried off, to be subsequently replaced by new mucous membrane. The muscular fibres developed in the uterine wall in such large quantities during pregnancy undergo rapid fatty degeneration and are absorbed, and in a few weeks the organ returns almost to its original size. The parturient woman is especially apt to take infectious diseases; and these, should they attack her, are fatal in a very large percentage of cases. Very special care should therefore be taken to keep all contagion from her.

There is a current impression that a pregnancy, once commenced, can be brought to a premature end, especially in its early stages, without any serious risk to the woman. That belief is erroneous. Premature delivery, early or late in pregnancy, is always more dangerous than natural labor at the proper term; the physician has sometimes to induce it, as when a malformed pelvis makes normal parturition impossible, or the general derangement of health accompanying the pregnancy is such as to threaten the mother's life; but the occasional necessity of deciding whether it is his duty to procure an abortion is one of the most serious responsibilities he meets with in the course of his professional work.

Dr. Storer, an eminent gynæcologist, states emphatically,

from extended observation, that despite apparent and isolated instances to the contrary—

1. A larger proportion of women die during or in consequence of an abortion, than during or in consequence of child-bed at the full term of pregnancy.

2. A very much larger number of women become confirmed invalids, perhaps for life; and—

3. The tendency to serious and often fatal organic disease, as cancer, is rendered very much greater at the so-called "turn of life," by previous artificially induced premature delivery.

During pregnancy there is a close connection between the placenta and uterus; nature makes preparation for the safe dissolution of this at the end of the normal period, but " its premature rupture is usually attended by profuse hæmorrhage, often fatal, often persistent to a greater or less degree for many months after the act is completed, and always attended with more or less shock to the maternal system, even though the full effect of this is not noted for years." The same authority states again: " Any deviation from this process at the full term " (i.e., the process, associated with lactation, by which the uterus is restored to its small non-gravid dimensions) " lays the foundation of, and causes, a wide range of uterine accidents and disease, displacements of various kinds; falling of the womb downwards or forwards or backwards, with the long list of neuralgic pains in the back, groin, thighs, and elsewhere that they occasion; constant and inordinate leucorrhœa; sympathetic attacks of ovarian irritation, running even into dropsy," etc., etc. There is, thus, abundant reason for bearing most things rather than the risks of an avoidable abortion.

Lactation. The mammary glands for several years after birth remain small, and alike in both sexes. Towards puberty they begin to enlarge in the female, and when fully developed form in that sex two rounded eminences, the *breasts*, placed on the thorax. A little below the centre of each projects a small eminence, the *nipple*, and the skin around this forms a colored circle, the *areola*. In virgins the areolæ are pink; they darken in tint and enlarge during the first pregnancy and never quite regain their original hue. The mammary glands are constructed on the compound racemose type. Each consists of from fifteen to twenty

distinct lobes, made up of smaller divisions; from each main lobe a separate *galactophorous duct*, made by the union of smaller branches from the lobules, runs towards the nipple, all converging beneath the areola. There each dilates and forms a small elongated reservoir in which the milk may temporarily collect. Beyond this the ducts narrow again, and each continues to a separate opening on the nipple. Imbedding and enveloping the lobes of the gland is a quantity of firm adipose tissue which gives the whole breast its rounded form.

During maidenhood the glandular tissue remains imperfectly developed and dormant. Early in pregnancy it begins to increase in bulk, and the gland lobes can be felt as hard masses through the superjacent skin and fat. Even at parturition, however, their functional activity is not fully established. The oil-globules of the milk are formed by a sort of fatty degeneration of the gland-cells, which finally fall to pieces; the cream is thus set free in the watery and albuminous secretion formed simultaneously, while newly developed gland-cells take the place of those destroyed. In the milk first secreted after accouchment (the *colostrum*) the cell destruction is incomplete, and many cells still float in the liquid, which has a yellowish color; this first milk acts as a purgative on the infant, and probably thus serves a useful purpose, as a certain amount of substances (biliary and other), excreted by its organs during development, are found in the intestines at birth.

Human milk is undoubtedly the best food for an infant in the early months of life; and to suckle her child is useful to the mother if she be a healthy woman. There is reason to believe that the processes of involution by which the large mass of muscular and other tissues developed in the uterine walls during pregnancy are broken down and absorbed, take place more safely to health if the natural milk secretion is encouraged. Many women refuse to suckle their children from a belief that so doing will injure their personal appearance, but skilled medical opinion is to the contrary effect; the natural course of events is the best for this purpose, unless lactation be too prolonged. Of course in many cases there are justifiable grounds for a mother's not undertaking this part of her duties; a physician is the proper person to decide.

In a healthy woman, not suckling her child, ovulation and

menstruation recommence about six weeks after childbirth; a nursing mother usually does not menstruate for ten or twelve months; the infant should then be weaned.

When an infant cannot be suckled by its mother or a wet-nurse an important matter is to decide what is the best food to substitute.   Good cow's milk contains rather more fats than that of a woman, and much more casein; the following table gives averages in 1000 parts of milk:

	Woman.	Cow.
Casein	28.0	54.0
Butter	33.5 ·	43.0
Milk sugar	44.5	42.5
Inorganic matters	4.75	7.75

The inorganic matters of human milk yield, on analysis, in 100 parts—calcinm carbonate 6.9; calcium phosphate, 70.6; sodium chloride, 9.8; sodium sulphate, 7.4; other salts, 5.3. The lime salts are of especial importance to the child, which has still to build up nearly all its bony skeleton.

When undiluted cow's milk is given to infants they rarely bear it well; the too abundant casein is vomited in loose coagula.   The milk should therefore be diluted with half or, for very young children, even two thirds its bulk of water. This, however, brings down the percentage of sugar and butter below the proper amount.   The sugar is commonly replaced by adding cane sugar; but sugar of milk is readily obtainable and is better for the purpose.   If used at all it should, however, be employed from the first; it sweetens much less than cane sugar, and infants used to the latter refuse milk in which milk sugar is substituted.   Cream from cow's milk may be added to raise the percentage of fats to the normal, but must be perfectly fresh and only added to the milk immediately before it is given to the child.   While milk is standing for the cream to rise it is very apt to turn a little sour; the amount of this sour milk carried off with the cream is itself no harm when mixed with a large bulk of fresh milk; it carries with it, however, some of the fungus whose development causes the souring, and this will rapidly develop and sour all the milk it is added to if the mixture be let stand.   As the infant grows older less diluted cow's milk may gradually be given; after the seventh or eighth month no addition of water is necessary.

In the first weeks after birth it is no use to give an infant starchy foods, as arrowroot.   The greater part of the starch

tional cases of accumulation of non-working adipose tissue) remains about the same until the climacteric. After that there is often an increase of weight for several years due mainly to increased formation of fat; a man's weight usually slowly increases until forty.

As old age comes on a general decline sets in, the rib cartilages become calcified, and lime salts are laid down in the arterial walls, which thus lose their elasticity; the refracting media of the eye become more or less opaque; the physiological irritability of the sense-organs in general diminishes; and fatty degeneration, diminishing their working power, occurs in many tissues. In the brain we find signs of less plasticity; the youth in whom few lines of least resistance have been firmly established is ready to accept novelties and form new associations of ideas; but the longer he lives, the more difficult does this become to him. A man past middle life may do good, or even his best work, but almost invariably in some line of thought which he has already accepted: it is extremely rare for an old man to take up a new study or change his views, philosophical, scientific, or other. Hence, as we live, we all tend to lag behind the rising generation.

Death. After the prime of life the tissues dwindle (or at least the most important ones) as they increased in childhood; it is conceivable that, without death, this process might occur until the Body was reduced to its original microscopic dimensions.

Before any great diminution takes place, however, a breakdown occurs somewhere, the enfeebled community of organs and tissues forming the man is unable to meet the contingencies of life, and death supervenes. " It is as natural to die as to be born," Bacon wrote long since; but though we all know it, few realize the fact until the summons comes. To the popular imagination the prospect of dying is often associated with thoughts of extreme suffering; personifying life, men picture a forcible and agonizing rending of it, as an entity, from the bodily frame with which it is associated. As a matter of fact, death is probably rarely associated with any immediate suffering. The sensibilities are gradually dulled as the end approaches; the nervous tissues, with the rest, lose their functional capacity, and, before the heart ceases to beat, the individual has commonly lost consciousness.

The actual moment of death is hard to define: that of the

Body generally, of the mass as a whole, may be taken to be the moment when the heart makes its last beat; arterial pressure then falls irretrievably, the capillary circulation ceases, and the tissues, no longer nourished from the blood, gradually die, not all at one instant, but one after another, according as their individual respiratory or other needs are great or little.

While death is the natural end of life, it is not its aim—we should not live to die, but live prepared to die. Life has its duties and its legitimate pleasures, and we better play our part by attending to the fulfilment of the one and the enjoyment of the other, than by concentrating a morbid and paralyzing attention on the inevitable, with the too frequent result of producing indifference to the work which lies at hand for each. Our organs and faculties are not talents which we may justifiably leave unemployed; each is bound to do his best with them, and so to live that he may most utilize them. An active, vigorous, dutiful, unselfish life is a good preparation for death; when that time, at which we must pass from the realm controlled by physiological laws, approaches, when the hands tremble and the eyes grow dim, when " the grasshopper shall be a burden and desire shall fail," then, surely, the consciousness of having quitted us like men in the employment of our faculties while they were ours to use, will be no mean consolation.

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